Movement ecology and fisheries bycatch risk of albatross and large petrel species from Bird Island, South Georgia

Black-browed albatrosses (cfrankish)

Caitlin Kim Frankish

Murray Edwards College

Department of Zoology

University of Cambridge

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DECLARATION

This thesis is the result of my own work and includes nothing which is the outcome of work done in collaboration except where specifically indicated in the text. It is not substantially the same as any that I have submitted, or, is being concurrently submitted for a degree or diploma or other qualification at the University of Cambridge or any other University or similar institution except as declared in the Preface and specified in the text. It does not exceed the prescribed word limit for the relevant Degree Committee (School of Biology).

Caitlin Kim Frankish

Cambridge

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SUMMARY

Recording animal movements is essential for understanding the distribution of species over time, with far-reaching consequences for fitness, population dynamics and conservation. Oceanic seabirds are some of the most mobile and threatened species on Earth, mainly because of incidental mortality (bycatch) in fisheries. Tracking these birds has improved our knowledge of how the environment and individual traits shape specific foraging and migratory strategies; however, this research is biased towards adult life-stages, which are easier to track. In particular, juveniles remain understudied, even though they are likely to differ in their critical habitats and overlap with fisheries, and hence bycatch risk, with implications for population trajectories. In this thesis, I capitalize on recent advances in tracking technology and the wealth of data collected on threatened albatross and large petrel species breeding at Bird Island, South Georgia, to investigate variation in spatial ecology and fisheries bycatch risk across multiple life-stages and species. In Chapter 1, I introduce the main topics of this thesis. In Chapters 2-4, I investigate how wind and resource availability shape divergent movement patterns between juveniles and adult life-stages, and identify age-specific bycatch risk. As high juvenile mortality is likely to result in an ageing population, in Chapter 5 I examine senescence in foraging behaviour, and consider the ramifications for population recovery. In Chapter 6, I then assess the effectiveness of existing fisheries bycatch mitigation measures by investigating the diving capabilities of the most bycaught species in the Southern Ocean. Finally, I conclude with a general discussion summarizing my main findings and suggesting future work. Overall, my results provide new insight into the capacity and motivation for movement in wide-ranging animals; highlighting the diversity of extrinsic and intrinsic processes shaping movements over the lifespans of individuals, and with implications for focusing conservation efforts in time and space.

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CHAPTER 1 – Introduction

1. 1 Tracking animal movements

In order to survive, animals may move in time and space to find food, mates or to avoid predators (Nathan 2008). Movements are furthermore constrained by an individual's physical capabilities (Vogel 2003) and are thought to be influenced by a range of processes that are internal (e. g. energetic requirements or breeding status; Haworth et al. 2006; Dunn et al. 2020) or external (e. g. weather or location of resources; Roshier et al. 2008; Evans et al. 2019). In particular, the location of resources can be patchy as environments are often heterogeneous and individuals are expected to optimize their movements to acquire food items in such a way that it maximizes their fitness (MacArthur & Pianka 1966; Fauchald 1999). Strategies can vary at the individual level and often differ among groups (e. g. age categories or sexes) or populations, reflecting specific foraging strategies related to habitat availability and preference (Kerches-Rogeri et al. 2020; Jaeger et al. 2014; Leimar et al. 2003). This variation has far-reaching consequences for population dynamics and conservation (Kristan III 2003; Samson et al. 2016).

Advances in tracking technologies in recent decades have revolutionized our knowledge of movements of individuals that would otherwise be difficult to observe; for instance, animals which fly or swim (Ropert-Coudert & Wilson 2005; Kays et al. 2015; Hays et al. 2016). These devices have revealed some of the amazing feats of which different species are capable (e. g. extensive migration distances, deep-diving capabilities or long flight durations; Egevang et al. 2010; Wienecke et al. 2006; Hedenström et al. 2016), and their continued development (miniaturisation, longer battery life and additional sensors) is providing increasingly complex and fine-scale ecological insights into different behaviours as well as their environmental context (Boehlert et al. 2001; Wilson et al. 2008; Williams et al. 2017). In parallel, statistical developments to take advantage of these extensive datasets allow testing of hypotheses relating

to observed trajectories and provide a more mechanistic understanding of what drives an animal to move from one location to another (Patterson et al. 2008; Mueller et al. 2011; Bauer & Klaassen 2013).

Movement data are also being used increasingly to inform the conservation of threatened wildlife (Fraser et al. 2018; Hays et al. 2019) . Due to the rapid and uncontrolled expansion of urban areas and human activities, mobile species are more likely to encounter a number of anthropogenic threats in their natural environment which may directly or indirectly affect their reproduction or survival (Ceballos & Ehrlich 2010; Little et al. 2016; Arcangeli et al. 2019). In addition, climate change as a result of human activities has the potential to alter the distribution and quality of habitats available to animals on broad spatial scales, with potentially dramatic consequences for their populations (Kelly & Goulden 2008; Johnson et al. 2011; Radchuk et al. 2019). As tracking studies are able to provide spatial context to the degree of overlap and interaction of animals with various pressures (Nabe-Nielsen et al. 2011; Queiroz et al. 2019; Thaxter et al. 2019), movement data can be used to design threat mitigation and improve the conservation status of a given species, for example by protecting its preferred foraging grounds or migratory routes (Pendoley et al. 2014; Choi et al. 2019; Handley et al. 2020).

1. 2 Spatial ecology of oceanic seabirds and fisheries bycatch

Marine animals have few natural barriers obstructing movement in their environment, and this is particularly true of oceanic seabirds which are free to roam across the world's seemingly 'featureless' oceans at low energetic cost (Croxall et al. 2005; Shaffer et al. 2006; Sachs et al. 2012). In addition, these wide-ranging birds regularly return to their breeding colonies where they are easier to monitor and catch in order to attach tracking devices, facilitating the collection of data on their movements in relation to intrinsic variables such as age, sex, breeding status etc. (Jouventin & Weimerskirch 1990; Wooller et al. 1992; Wakefield et al. 2009a). For these reasons, they are ideal study species for investigating ecological questions relating to the

processes driving different habitat preferences and movement strategies across wide spatial scales during the breeding and nonbreeding seasons. This information is of high conservation value given oceanic seabirds are a highly threatened group of birds and used as indicator species of marine ecosystem health (Mallory et al. 2010; Phillips et al. 2016; Dias et al. 2019).

Tracking oceanic seabirds has shown that these birds are capable of travelling incredible distances (e. g. up to 15,000 km during a single foraging trip; Jouventin & Weimerskirch 1990), but that individuals show distinct preferences for a range of dynamic and static oceanographic features which concentrate prey at varying spatial and temporal scales (e. g. fronts, sea-ice, upwelling zones; Grémillet et al. 2015; Cox et al. 2016; Scales et al. 2016). These birds employ a range of techniques for locating foraging patches and acquiring prey, such as area-restricted search, spatial memory or local enhancement (Fauchald & Tveraa 2003; Regular et al. 2013; Thiebault et al. 2014). They use some areas predictably and others more opportunistically depending on habitat availability, dietary preferences or environmental conditions (Montevecchi et al. 2009; Kowalczyk et al. 2015; Afán et al. 2021), and these strategies differ throughout the year based on changing internal and external conditions (Phillips et al. 2006; Quillfeldt et al. 2013; Clay et al. 2017). There is still however an incomplete understanding of how specific strategies develop and change over the lifespan of individuals and filling this gap is a fundamental goal in movement ecology (Nathan et al. 2008; Hazen et al. 2012; Hays et al. 2016).

As seabirds breed on land but forage at sea, they are exposed to a large number of threats (e.g. pollution, invasive species, overfishing, competition with fisheries for food or incidental mortality in fisheries) and the management of wide-ranging pelagic species requires complex transboundary collaboration (Wanless et al. 2009; Cury et al. 2011; Grémillet et al. 2018b; Dias et al. 2019; Mills et al. 2020a). Incidental mortality (bycatch) in industrial pelagic or demersal longline, trawl or artisanal fisheries is however by far the biggest threat to the

survival of many species as these birds overlap in distribution with fishing vessels at their foraging grounds, and discards (spent bait, offal and unwanted catch) provide an easy source of food (Anderson et al. 2011; Phillips et al. 2016). Mortality occurs in a number of ways; birds can become entangled while diving for prey in gillnet fisheries, are injured in collisions with trawl cables, or become hooked on baited hooks and drown when the line sinks in longline fisheries, with devastating consequences for many populations (Brothers 1991; Waugh et al. 2011; Barbraud et al. 2012). Tracking seabirds has provided important insights into the overlap of different species with the distribution of fishing vessels, thereby highlighting regions and seasonal periods during which they are most vulnerable (Genovart et al. 2018; Clay et al. 2019; Carle et al. 2019). However, these assessments are mostly limited to adults, which are easier to track, and the susceptibility of other age classes to bycatch remains a major knowledge gap that it is essential to fill in order to focus mitigation (Gianuca et al. 2017; Clay et al. 2019; Carneiro et al. 2020).

1. 3 Study site and study species

Bird Island, South Georgia (54°00'S, 38°03'W), is a small (4.8 km long and max. 800 m wide) subantarctic island in the southwest Atlantic Ocean, and home to one of the world's densest aggregations of breeding seabirds (Croxall & Prince 1980). The island, which is part of the South Georgia archipelago within the United Kingdom Overseas Territory of South Georgia and the South Sandwich Islands, is located 300 km south of the Antarctic Polar Front in a remarkably productive and windy oceanographic region, which provides favourable foraging and flight conditions for pelagic albatross and petrel species (Figures 1.1 and 1.2; Pennycuick 1982a; Atkinson et al. 2001). Populations of these birds have been the subject of long-term monitoring studies since the 1950s (Tickell et al. 1965; Croxall et al. 1990; Pardo et al. 2017) conducted mostly by the British Antarctic Survey, and in this thesis, I analyse data collected from three species breeding at this site (Figure 1.3); the black-browed albatross (*Thalassarche*

melanophris), grey-headed albatross (*Thalassarche chrysostoma*) and white-chinned petrel (*Procellaria aequinoctialis*). These birds are long-lived and wide-ranging, and their breeding populations at South Georgia are of global importance (Martin et al. 2009; Poncet et al. 2017).

Tracking studies conducted since the mid-1980s have provided a comprehensive overview of the spatial ecology of oceanic seabirds breeding on Bird Island in terms of space use and other aspects of foraging behaviour at sea (e. g. diving ability and diurnal activity patterns; Phillips et al. 2008). During the breeding season, albatrosses and petrels are subject to central-place foraging constraints and remain within a few days flight of the colony (Phillips et al. 2004c, 2005a, 2006; Jiménez et al. 2016). While the three species studied in this thesis have a similar breeding phenology (the birds arrive at South Georgia in September-November and depart after breeding in April-May; Hall 1987; Prince et al. 1994b), they differ in their at-sea distributions during this period and feed on varying combinations of fish, squid and krill (Croxall et al. 1995; Berrow & Croxall 1999; Mills et al. 2020b). Indeed, white-chinned petrels mainly forage either on the Patagonian Shelf, the Antarctic Polar Frontal zone or further south (Berrow et al. 2000b; Phillips et al. 2006), while black-browed albatrosses primarily feed along the north Scotia Arc and the Scotia Sea and grey-headed albatrosses in the Polar Frontal Zone and Scotia Sea (Phillips et al. 2004c).

In contrast, many of the oceanic seabirds breeding at South Georgia disperse more widely across the Southern Ocean during the non-breeding season (Phillips et al. 2005b; Clay et al. 2016, 2018). This is especially true for the albatrosses studied in this thesis; black-browed albatrosses target the Benguela Upwelling region, the Patagonian Shelf or the waters surrounding Australia and grey-headed albatrosses oceanic waters in the Southwest Atlantic, Southwest Indian and Pacific oceans and the Patagonian Shelf (Phillips et al. 2005b; Croxall et al. 2005). As for white-chinned petrels, adults mainly winter at the Patagonian Shelf and to a lesser extent at the Humboldt Current near Chile (Phillips et al. 2006). It is thus clear that

species show broad preferences for certain oceanographic regions, but there can be high individual variability in patterns of space use and at-sea activity patterns, and more research is needed to determine the intrinsic and extrinsic drivers (Phillips et al. 2004c; Croxall et al. 2005; Clay et al. 2016). The accumulation of extensive multi-species demographic and tracking data at Bird Island, including the deployment of multiple types of loggers on individuals differing in sex, age and breeding status, provided the opportunity in this thesis to gain a more detailed understanding of at-sea behaviour across multiple life-stages.

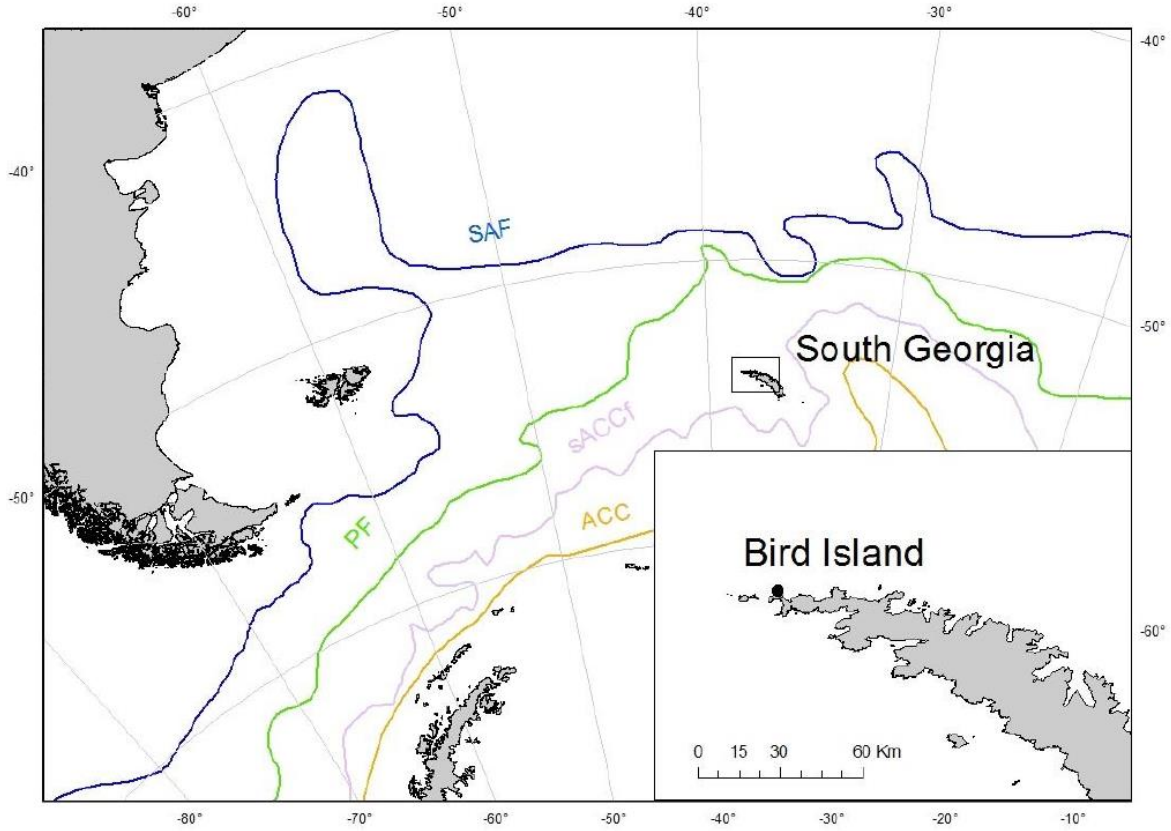

Figure 1.1: Location of Bird Island (inset) and South Georgia in relation to oceanicfronts (SAF is the subAntarctic Front, PF is the Polar Front, sACCf is the southern Antarctic Circumpolar Front and the ACC is the Antarctic Circumpolar Current).

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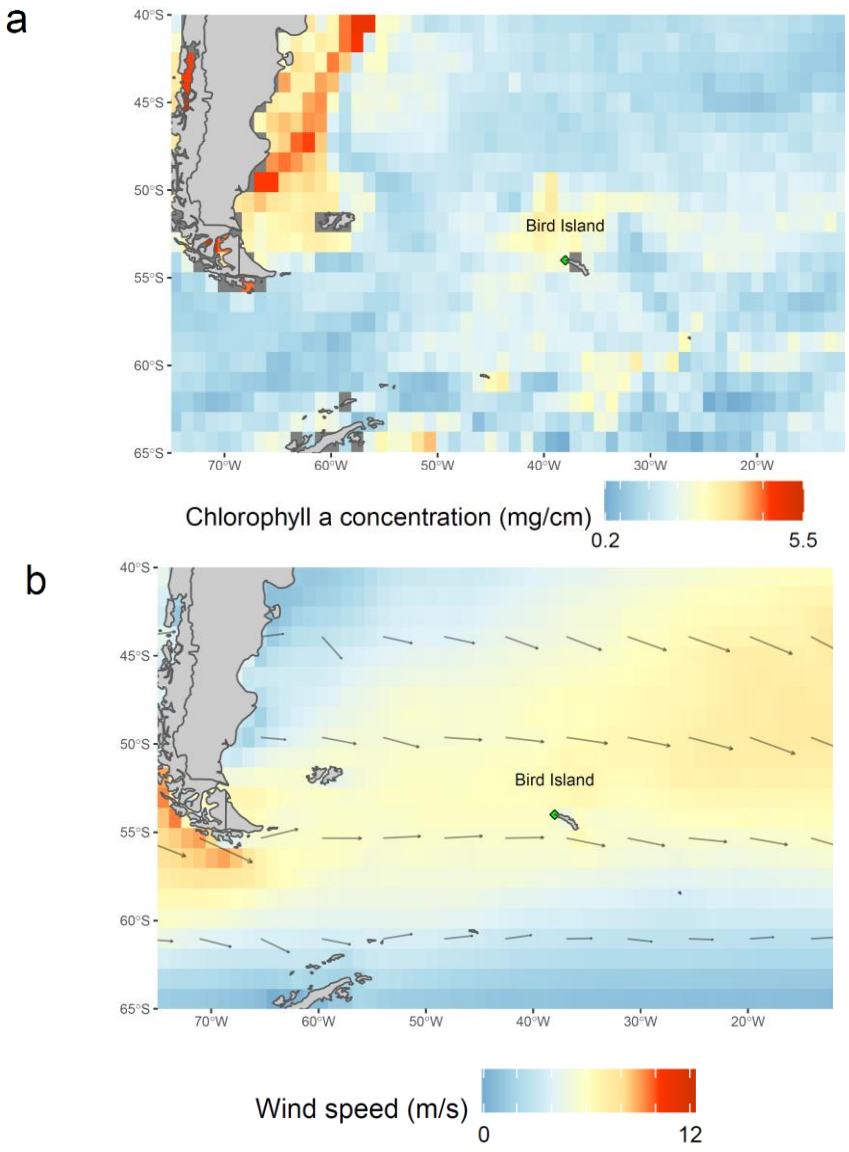

Figure 1.2: Environmental conditions around South Georgia; a) average decadal productivity in December (2010-2020) calculated using monthly chlorophyll a concentration data obtained from the GlobColour-merged chlorophyll a product disseminated via the Copernicus Marine Environmental Monitoring Service (Garnesson et al. 2019; accessed March 2021) at 0.04° spatial resolution and b) average decadal wind speed and direction (represented by arrows) in December (2010-2020) calculated using monthly zonal and meridional wind components downloaded from the European Centre for Medium Range Weather Forecasts (ECMWF) ERA5 reanalysis dataset (https://doi.org/10.24381/cds.f17050d7; accessed March 2021) at 0.25° spatial resolution.

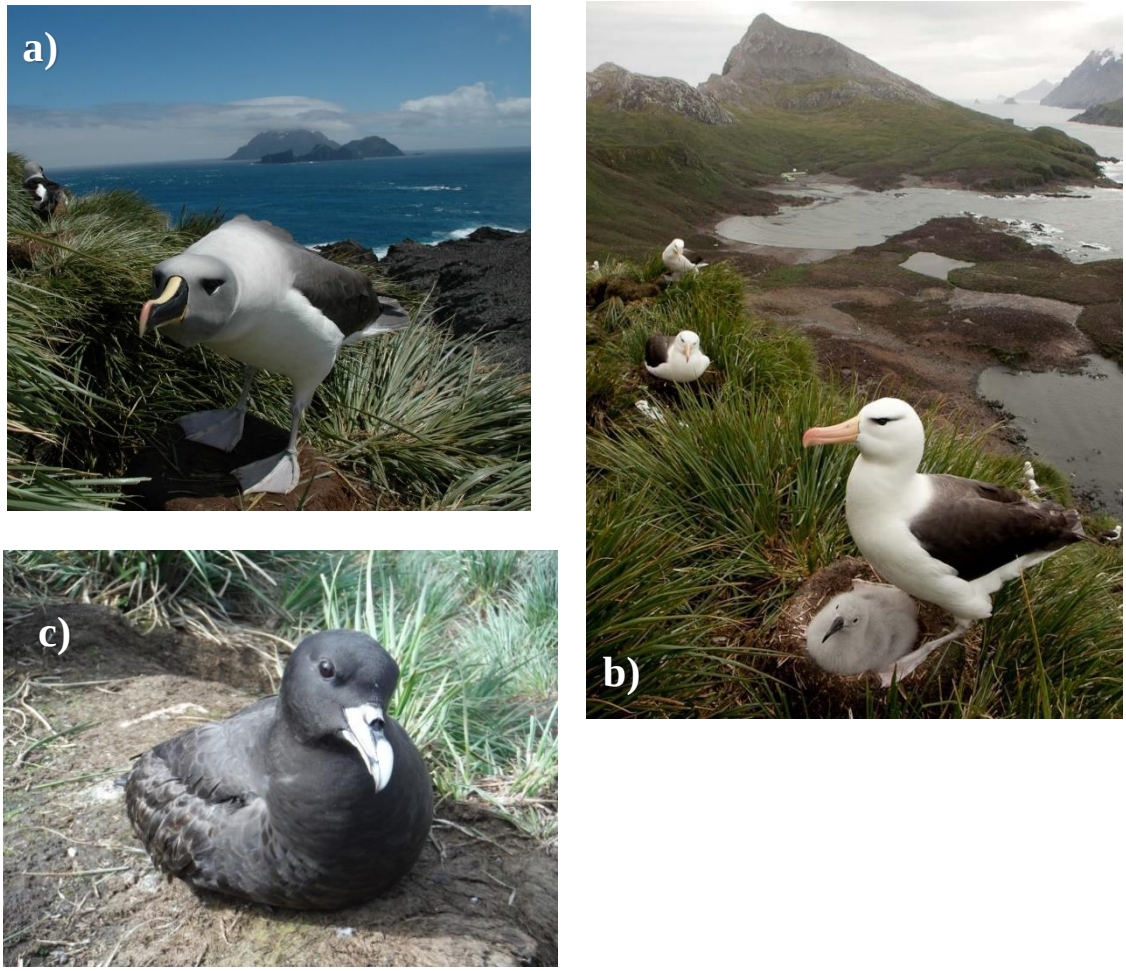

Figure 1.3: Study species: a) grey-headed albatross (*Thalassarche chrysostoma*), b) black-browed albatross (*Thalassarche melanophris*) and c) white-chinned petrel (*Procellaria aequinoctialis*). Photographs were taken by Richard Phillips.

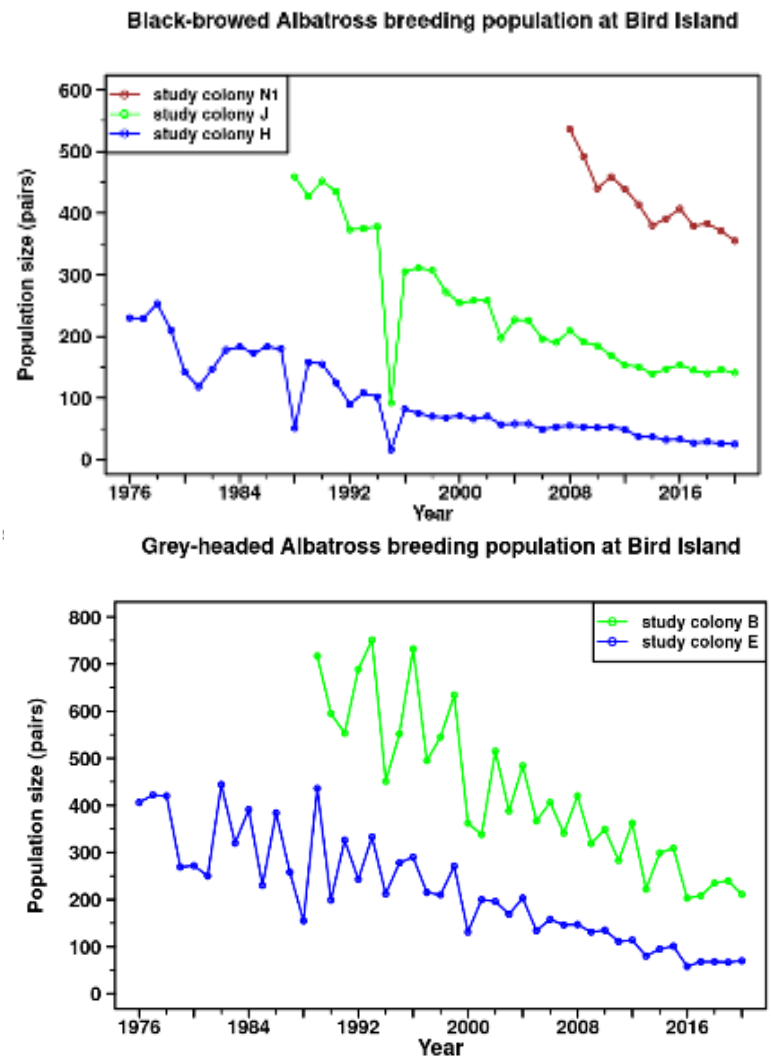

Figure 1.4: Change in the number of breeding pairs of black-browed (top) and grey-headed (bottom) albatrosses (*Thalassarche melanophris* and *T. chrysostoma*) since 1976 at several colonies on Bird Island, South Georgia, monitored by the British Antarctic Survey.

Finally, the populations of albatrosses and large petrels at South Georgia were historically subject to high rates of incidental mortality (bycatch) during the breeding season as a result of negative interactions with demersal longline fishing vessels targeting Patagonian Toothfish *(Dissostichus eleginoides*) in the vicinity of South Georgia during the austral summer (Dalziell & Poorter 1993). In the 1990s, the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR) put in place a string of mitigation measures (seasonal closures,

the requirement for on-board scientific observers, night-setting, heavier line-weighting and use of bird-scaring lines) which successfully reduced bycatch to negligible levels in the region (Croxall 2008; Bestley et al. 2020). Numbers of breeding pairs of albatrosses and white-chinned petrels are, however, still declining, as these birds overlap in distribution with fishing fleets further afield (Figure 1.4; Martin et al. 2009; Poncet et al. 2017; Clay et al. 2019) . The white-chinned petrel is the most bycaught species in the Southern Ocean and the two albatross species studied in this thesis are designated as Priority Populations for conservation efforts by the Agreement on the Conservation of Albatrosses and Petrels (ACAP) (ACAP, www.acap.aq; Phillips et al. 2016). While there are comprehensive year-round data on overlap of adults and fisheries (Clay et al. 2019), there is still little information on the exposure of young life-stages (juveniles and immatures) to this threat even though they may be more vulnerable due to differing distributions or naïve foraging behaviours (Gianuca et al. 2017).

1. 4 Overview of methods

This thesis examines tracking data collected using several devices which differ in the type and accuracy of information recorded: Platform Terminal Transmitters (PTTs), Global Positioning System (GPS), light-level geolocators (Global Location Sensor or GLS loggers) and Time-Depth Recorders (TDRs). PTTs send radio signals to Argos receivers on polar-orbiting satellites from which location is determined according to the Doppler shift in transmission frequency as the satellites move relative to the PTT (Argos 1996). There is therefore no need to recover the tag but locations are degraded by poor satellite visibility and high tag speeds, resulting in temporal gaps in data and varying spatial errors (< 1 km up to several 100 km depending on the location class and the error percentile used to estimate location accuracy; Nicholls et al. 2007; Soutullo et al. 2007; Douglas et al. 2012). In contrast, GPS tags reliably record location data at high temporal resolutions (up to 1 Hz) and with little spatial error (a few metres), allowing fine-scale information to be inferred from movement (Weimerskirch et al.

2007). GLS loggers record ambient light, from which location data can be inferred from thresholds in light curves but at much coarser spatial and temporal resolutions; two locations per day with an average spatial accuracy of 186 ± 114 km (Phillips et al. 2004a). Their battery requirements are however very low, allowing researchers to record movements over several years (Yamamoto et al. 2014). Combined GLS-immersion loggers also record saltwater immersion, providing complimentary information on at-sea activity patterns, which at highest resolution include the timing and duration of all flights and periods spent on the water (Phalan et al. 2007; Mackley et al. 2011). Finally, TDRs provide timing, duration and depths of dives from analysis of pressure data (Dean et al. 2013).

Tracking data can be used to broadly quantify movement characteristics and abilities (Wienecke et al. 2006; Phalan et al. 2007; Egevang et al. 2010). They can also be the basis of more complex investigations of resource selection and habitat use (Awkerman et al. 2005; Suryan et al. 2006; Wakefield et al. 2011), which is a primary research goal in ecology (Johnson 1980; Boyce et al. 2002). There are a large number of statistical models available for understanding the distribution of animals in relation to remotely-sensed environmental data, and deciding which approach is most appropriate may depend on the research questions and type of data available (Guisan & Zimmermann 2000; Hao et al. 2019; Melo-Merino et al. 2020). Methods which take into account the habitat available to an animal, i.e. located within its movement capability, are thought to provide a more realistic quantification of preferred types of habitat (Matthiopoulos 2003; Aarts et al. 2008; Wakefield et al. 2009a) and result in reasonable predictions of individual and population-level space use (Clay et al. 2016; Scales et al. 2016; Baylis et al. 2019). These tools furthermore allow non-normal responses of animals to their environments which may be particularly useful in marine habitats where foraging opportunities arise at varying spatial and temporal scales (Prince et al. 1999; Fritz et al. 2003; Wakefield et al. 2011). Mechanistic frameworks, which simulate or model movements as

discrete steps characterized by unique displacement rates and turning angles, are also becoming increasingly popular as they allow researchers to explore the potential processes driving sequential movement patterns as opposed to quantifying average preferences for specific types of habitats (Mueller et al. 2011; Bauer & Klaassen 2013; Revell & Somveille 2017).

The other datasets used in this thesis are on the distribution of longline fishing effort, which I use to assess the potential bycatch risk of the tracked albatrosses and petrels. Longline fishing effort (number of hooks deployed or hours spent fishing in pelagic and demersal longline fisheries) is recorded in log-books and reported to regional fisheries management organizations or national fishing agencies (McCluskey & Lewison 2008). While this data is widely used in research, it can suffer from reporting inaccuracies, is not always freely-available and its resolution is coarse compared with the spatial and temporal scales at which seabirds can be tracked (Tuck et al. 2003; Torres et al. 2013; Ewell et al. 2020). For example, pelagic longline effort for some fisheries is reported as number of hooks deployed per month or quarter and 5 x 5° grid cell (Clay et al. 2019). Alternatively, the recently-developed Global Fishing Watch dataset provides daily fishing effort (hours) of vessels transmitting their location using an automatic identification system (AIS) between 2012 and 2020 (www.globalfishingwatch.org; Kroodsma et al. 2018). While AIS transmitters are only fitted to 50-75% of active vessels that are over 24 m in length, this dataset has the potential to revolutionize our ability to track fishing across the world's oceans in an independent and standardized manner, and carry out fine-scale bycatch risk assessments for seabirds as well as other vulnerable marine predators (McCauley et al. 2016; Kroodsma et al. 2018; Shepperson et al. 2018; Sala et al. 2018; Queiroz et al. 2019).

1. 5 Thesis aims and structure

The major aims of this thesis are to:

- (1) characterize the movements and foraging behaviour of juvenile albatross and petrel species fledged from Bird Island, South Georgia
- (2) determine the drivers of variation within and among species in movement patterns, with a focus on age, breeding status, sex and the environment
- (3) consider the implications of variation in movement strategies for life-history theory, fisheries overlap and bycatch mitigation

In **Chapter 2**, I describe the previously unknown initial movements (8 weeks) of white-chinned petrels fledging from Bird Island, and contrast their movement characteristics and flight capabilities with those of non-breeding adults. I also apply a mechanistic movement model to investigate the extent to which environmental processes (winds and chlorophyll a concentration; a proxy for food resources) drive their divergent distribution patterns, and determine the implications for age-specific longline fisheries bycatch risk. This study provides new insights into the ontogeny of movement strategies in a very long-lived species and has important implications for the conservation of this threatened population.

In **Chapter 3**, I investigate how juvenile movements and foraging behaviour change over time (four months) using tracking data from grey-headed albatrosses which fledged in 2018 and 2019 from Bird Island. Specifically, I use integrated step-selection analysis to determine whether juveniles show a progression in their movement characteristics and response to local environmental conditions (winds and productivity). By using a mechanistic framework, this study highlights the importance of external cues in driving behavioural decisions in naïve individuals, with important implications for understanding how environmental change may impact the future migratory patterns of oceanic seabirds.

In **Chapter 4,** I compare monthly at-sea distributions of juvenile grey-headed albatrosses with those of adults in order to assess stage-specific bycatch risk in pelagic longline fisheries.

In particular, I determine whether an apparent bycatch hotspot for grey-headed albatrosses reported by Japanese observers in the central-southeast Atlantic Ocean is in a region used in particular by young individuals from South Georgia. If so, this would have important implications for understanding the sustained decline of this globally-important population. Results from this study emphasize the importance of uncovering the cryptic life-stages, or 'lost-years', of marine megafauna for focusing conservation efforts.

High juvenile mortality is likely to result in an ageing population, and the ability of seabird populations to recover will depend on the behaviour of older age classes. In **Chapter 5**, I perform a cross-sectional study to investigate the links between age, foraging behaviour and breeding stage in two species of albatrosses; grey-headed and black-browed albatrosses tracked from Bird Island over two decades. Results from this study highlight the complex interaction between intrinsic and extrinsic factors in determining individual foraging strategies during the energetically-demanding breeding season, and that changes in foraging efficiency or distribution with age may reduce the ability of populations to withstand worsening environmental conditions.

In **Chapter 6**, I assess the likely effectiveness for mitigating bycatch of alternative measures currently in use in longline fisheries by investigating the diving behaviour and activity patterns of the most bycaught seabird in the Southern Ocean, the white-chinned petrel. Specifically, I use three data sources (dives, spatial movements and immersion events) to examine diverse aspects of at-sea foraging behaviour. Results from this study underline the opportunistic foraging abilities of this threatened seabird and are discussed in the context of the design of effective bycatch mitigation procedures; appropriate line-weighting, bird-scaring line configuration and use of night-setting.

In **Chapter 7**, I summarize the findings from the previous chapters and discuss how these results fill important knowledge gaps relating to the distributions and behaviour of threatened seabirds, thereby furthering our ecological understanding of the processes shaping movement strategies and exposing individuals to bycatch in fisheries. I also suggest opportunities for future research on key topics in movement ecology as well as for the conservation of mobile species such as oceanic seabirds.

CHAPTER 2 - Environmental drivers of movement in a threatened seabird: insights from a mechanistic model and implications for conservation

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Author contributions:

I conceived the project, developed the research questions, conducted the data analysis and wrote up the chapter with supervision from R. A. Phillips & A. Manica.

T. A. Clay provided help with coding the fisheries overlap analysis in R (see section 2. 3. 3 of the methods) and feedback on various versions of this manuscript.

M. Somveille provided advice on how to run the mechanistic model used in this chapter (see section 2. 3. 2) and feedback on various versions of this manuscript, in particular on all sections pertaining to the mechanistic movement model.

ABSTRACT

Aim: Determining the drivers of movement of different life-history stages is crucial for understanding age-related changes in survival rates and, for marine top predators, the link between fisheries overlap and incidental mortality (bycatch), which is driving population declines in many taxa. Here, I combine individual tracking data and a movement model to investigate the environmental drivers and conservation implications of divergent movement patterns in juveniles (fledglings) and adults of a threatened seabird, the white-chinned petrel (*Procellaria aequinoctialis*).

Location: South-west Atlantic Ocean.

Methods: I compare the spatial distributions and movement characteristics of juvenile, breeding and non-breeding adult petrels, and apply a mechanistic movement model to investigate the extent to which chlorophyll a concentrations (a proxy for food resources) and ocean surface winds drive their divergent distribution patterns. I also consider the conservation implications by determining the relative overlap of each life-history stage with fishing intensity and reported fishing effort (proxies for bycatch risk).

Results: Naïve individuals fledged with similar flight capabilities (based on distances travelled, flight speeds and track sinuosity) to adults but differed in their trajectories. Comparison of simulations from the mechanistic model with real tracks showed that juvenile movements are best predicted by prevailing wind patterns, whereas adults are attracted to food resources on the Patagonian Shelf. The juveniles initially dispersed to less productive oceanic waters than those used by adults, and overlapped less with fishing activity; however, as they moved westwards towards South America, bycatch risk increased substantially.

Main Conclusions: The use of a mechanistic framework provided insights into the ontogeny of movement strategies within the context of learned versus innate behaviour and demonstrated that divergent movement patterns of adults and juveniles can have important implications for the conservation of threatened seabirds.

2. 1 Introduction

Determining the processes that influence the capacity and motivation for movement within and among species constitutes a primary goal for ecologists, given the far-reaching consequences for individual fitness, population dynamics and conservation (Munday 2001; Ribera et al. 2003; Arjo et al. 2007). In most animals, the mechanisms shaping the initial movements of juveniles away from their natal grounds and subsequent habitat use are poorly known, yet this period represents a critical life-history stage when mortality is high (Victor 1986; Owen & Black 1989; Gaillard et al. 1998). Naïve individuals need to acquire foraging, navigation and other skills, and are physically immature, yet must learn how to survive in an unknown and often hostile environment (Gyuris 1994; Avens 2004; Daunt et al. 2007a; Riotte-Lambert & Weimerskirch 2013). In addition, young animals may differ from older life-stages in terms of their morphology, nutrient requirements or competitive abilities, and, consequently, may exploit distinct habitats (Stamps 1983; Stockhoff 1993; Simonović et al. 1999). Understanding these age-related behavioural differences is a priority for research and conservation, especially in species that undertake large-scale dispersive movements (Graham et al. 2006; Arthur et al. 2008; Hazen et al. 2012).

Recent advances in tracking technologies have facilitated studies that shed light on the initial movement patterns of both terrestrial and marine species (Hazen et al. 2012; Kays et al. 2015). Tag miniaturization means devices can be attached to smaller, and hence younger individuals, and improved data storage and transmission capabilities has provided increasing coverage of the ‘lost-years’ for long-lived animals (Fedak 2002; Ciucci et al. 2009; Shillinger et al. 2012a; Mansfield et al. 2014). Juveniles sometimes follow directed movement paths with low among-individual variation, suggesting innate navigation capabilities (Avens 2004; Putman et al. 2014). In contrast, other species exhibit high individual variability in displacement patterns, with idiosyncratic paths indicative of a period of learning or

exploration (Ferrer 2008; Guilford et al. 2011; de Grissac et al. 2016). In both instances, decisions made by young age classes of when and where to move are strongly linked to external cues, yet few studies have explored the environmental drivers of juvenile movements, and most were correlative (Werner et al. 1981; Riotte-Lambert & Weimerskirch 2013; Igulu et al. 2014). A mechanistic approach may offer a useful framework for testing hypotheses about the ecological drivers shaping the distribution of different life-history stages (Moorcroft et al. 2006; Somveille et al. 2015; Merkle et al. 2019).

Compared to the terrestrial realm, there are relatively few barriers to movement in the marine environment (Caizergues & Ellison 2002; Alderman et al. 2010; Long et al. 2010; Mansfield et al. 2014). In particular, oceanic seabirds often conduct extremely large-scale movements due to their ability to exploit wind gradients, leading to very low flight costs (Weimerskirch et al. 2000b, 2006; de Grissac et al. 2016). They are fascinating models for studying juvenile movement patterns, as juveniles are abandoned by their parents at fledging; naïve individuals must thus learn how to forage and navigate effectively in a seemingly featureless ocean in which resources are patchily distributed (Ashmole 1963; MacLean 1986). Tracking studies indicate that juveniles of some species disperse away from their colony with similar movement capabilities and using broadly the same routes as adults, which generally target seasonally productive foraging habitats (Yoda et al. 2004; Péron & Grémillet 2013; Mendes et al. 2017). Recent research suggests that in oceanic seabirds, juveniles may have an innate ability to make favourable use of winds (Weimerskirch et al. 2006; Riotte-Lambert & Weimerskirch 2013). However, they may still differ from adults in terms of speed, sinuosity, direction, distance travelled or habitat use, suggesting that contrasting drivers underpin age-specific movement patterns (Kooyman & Ponganis 2007; Trebilco et al. 2008; Ismar et al. 2010; Hatch et al. 2011; Thiers et al. 2014). As individuals of all ages must acquire resources from their environment in order to survive, the availability and accessibility of productive

foraging habitats may place important constraints on movement, with major implications for mortality rates of different life-history stages (Wakefield et al. 2009a; Alderman et al. 2010; Clay et al. 2019).

The white-chinned petrel (*Procellaria aequinoctialis*) is a wide-ranging, oceanic seabird, listed as Vulnerable on the IUCN Red List (Phillips et al., 2016). While the year-round adult distribution has been investigated, less is known about the foraging behaviour of juveniles, despite the priority for conservation given ongoing population declines at most breeding sites (Phillips et al., 2016). Thirteen juveniles tracked from Kerguelen and Crozet Islands (southern Indian Ocean) travelled similar distances away from their natal sites as migrating adults, but settled in separate areas (Péron et al. 2010; de Grissac et al. 2016). Such results underline that juveniles may face differential mortality pressures, particularly relating to incidental mortality (bycatch) in demersal and pelagic longline fisheries, which represents the greatest at-sea threat to many seabirds (Clay et al. 2019; Dias et al. 2019; Carneiro et al. 2020). Nonetheless, the environmental drivers of movements of juvenile white-chinned petrels and their overlap with fisheries have not been quantified.

Here, I analysed movement data from juvenile and adult white-chinned petrels tracked from South Georgia, southwest Atlantic Ocean, which is the largest global population and is declining (Berrow et al. 2000a), to: (1) investigate initial dispersal patterns of juveniles during the post-fledging period; (2) apply a mechanistic movement model to identify the potential drivers of movement patterns of different life-history stages, and; (3) determine relative overlap with longline fisheries of juveniles and adults, and the implications for conservation using vessel tracking data from the open-source, high-resolution Global Fishing Watch dataset (Global Fishing Watch [GFW] 2019) and fishing effort for tuna and other billfishes reported to the International Commission for the Conservation of Atlantic Tunas (ICCAT). South Georgia lies in the path of prevailing westerly winds, and thus the main

wintering site for this population, the Patagonian Shelf, is directly accessed by flying into headwinds, which is energetically costly (Weimerskirch et al. 2000b; Phillips et al. 2006). This study system therefore offers an ideal opportunity to investigate the relative influence of different environmental factors on long-distance movement in birds; attraction to foraging resources, and the effect of wind on energetic costs of movement (Somveille et al. 2015; Vansteelant et al. 2017b). I hypothesize that wind speed and direction is more likely to determine the trajectories of naïve individuals with no prior flight or foraging experience, whereas experienced adults should migrate directly towards known foraging areas.

2. 2 Methods

2. 2. 1 Deployments and tracking data processing

All birds were tracked from Bird Island (54°00'S, 38°03'W), South Georgia, during the 2014/15 breeding season and subsequent winter. Telonics TAV-2630 satellite transmitters (Platform Terminal Transmitters, PTTs) with a duty cycle of 8h ON and 44h OFF, were deployed on 13 white-chinned petrel chicks on 15 April 2015 to track at-sea movements in the few months post-fledging. These provided locations on average every hour during ON periods. Fifteen breeding adults were fitted with i-gotU GPS loggers (Mobile Action Technology Inc., New Taipei City, Taiwan) during incubation in December 2014, and devices retrieved on subsequent nest visits during daytime. GPS loggers were set to record every 30 min. Three GPS devices were not retrieved because the nest failed or the chick hatched by the time the bird returned. Both PTTs and GPS loggers were attached with Tesa ® tape to back feathers. Sixteen birds (including nine of those that had been tracked with GPS) were equipped with an Intigeo C250 geolocator (Global Location Sensor or GLS logger; Migrate Technology Lt, Cambridge, UK) between 15 December 2014 and 13 January 2015 to track movements during the subsequent non-breeding period. Geolocators were attached by

cable-tie to a plastic leg ring, and all devices were retrieved in the following austral breeding season (14 December 2015 to 7 January 2016). The loggers measured light in the range of 1.1 to 74418 lux (maximum recorded at 5 min intervals), temperature every 20 minutes of continuous wet (maximum, minimum and mean saved every 4 h), and tested for saltwater immersion every 6 s. The immersion data were used for generating the speed parameters used in the processing of tracks from non-breeding adults (see below, Table S1.1). In all cases, the total mass of devices including attachments were less than the 3% threshold of body mass beyond which deleterious effects are more common in oceanic seabirds (Phillips et al. 2003).

PTT and GPS tracks were processed using an iterative forward/backward-averaging filter (McConnell et al. 1992) to remove any locations which required sustained flight speeds above 80 $km.h^{-1}$ (Berrow et al. 2000b). Data from GPS loggers and PTTs (during the ON periods only) were interpolated at hourly intervals to obtain regular positions, as this time step represented the coarsest tracking interval across datasets. GPS tracks from breeding adults were resampled to the same duty cycle as the tracks from juveniles in order to compare movement parameters between these life-history stages using an equivalent sampling regime.

Locations were estimated for adults tracked during the non-breeding period using the raw light intensities from the geolocators processed according to Merkel et al. (2016, see Appendix S1 for details). GLS data were not interpolated, as the estimated locations correspond to local midday and midnight. Juvenile tracks were resampled to 12-hour intervals to allow for comparisons of their movement parameters with those of the non-breeding adults. GLS locations were cropped to the juvenile departure dates from the colony to allow for the comparison of utilization distribution and overlap with fishing effort.

2. 2. 2 Comparing movements and distributions between life-history stages

I compared the spatial distributions and movement characteristics (maximum range and average longitude; metrics #1 and #2 below) of juveniles and non-breeding adults at large spatial scales based on the twice-daily fixes from the PTTs and geolocators, and the movement characteristics (speed and track sinuosity; metrics #3 and #4 below) at small spatial scales based on the hourly-interpolated PTT fixes and the GPS data from incubating adults, respectively (see above). The movement metrics were those commonly used for analyses of animal trajectories (Calenge et al. 2009); (1) Maximum range (maximum distance from the colony in km, calculated using function 'spDistsN1' in package 'sp'), (2) Longitude averaged over weekly time periods for juveniles, and for the first 8 weeks, post-departure, of non-breeding adults (corresponding to the maximum duration of a juvenile track; 57 days); (3) Speed (in $km.hr^{-1}$) and (4) track sinuosity (calculated as follows: $\boldsymbol{S = 1 - D_a / D_b}$, with $\boldsymbol{D_a}$ the beeline distance between the first and last location of every 'ON' portion of the trip and $\boldsymbol{D_b}$ the real distance travelled between the two locations). Speed and track sinuosity were also averaged over a weekly time period for juveniles to examine changes over time, as with metrics #1 and #2. Speed was square-root transformed to improve data spread.

Linear mixed-effects models were run with each movement metric as the response variable and individual ID as a random effect, testing for differences between life-history stages as a function of time. For models with maximum range and longitude, the covariates included life-history stage (a factor with two levels; non-breeding adult *NB*, and juvenile *JUV*), weeks since departure from the colony (*WEEK*; factor with eight-levels; 1-8), and their interaction. For models with speed and sinuosity, covariates included life-history stage (a factor with two levels; incubating *INC* adults, and juvenile *JUV*). Weekly differences were further investigated in juveniles only, where *WEEK* was again included as a factor with eight levels

(1-8), to test whether juveniles showed signs of learning in terms of their flight abilities. For each model set, all possible combinations of predictors were computed and models were ranked according to Akaike Information Criterion (AICc) values, where the most supported model(s) were considered to be those within 2Δ AICc of the top model (Burnham & Anderson 2004). Candidate models were excluded from this set if there were simpler nested versions with lower ΔAICc values (Arnold 2010).

To determine if juvenile and non-breeding adult white-chinned petrels differed in their weekly spatial distributions, I calculated utilization distribution (UD) kernels using the R package *'*adehabitatHR*'* (Calenge 2006). I first carried out a re-sampling procedure to determine whether sample sizes were large enough to represent population-level space use (Tables S1.2 & S1.3 and Fig. S1.1; Clay et al. 2019). This was not the case, and therefore the subsequent analysis represents the utilization hotspots of the sampled individuals rather than the population. Plots of the increase in kernel area with isopleth level for each individual, stage and week, indicated that the 61% isopleth was the most appropriate for weekly cross-stage comparisons of core area, and the 95% isopleth best-represented the general use area (Fig. S1.2 and Table S1.4; Vander Wal & Rodgers 2012). To control for differences in individual track duration, separate UDs were generated weekly for each bird, and then weighted by the proportion of locations from each bird with respect to the total number for all birds for a given stage-week combination. Weighted individual UDs were then summed to create weekly UDs for each life-history stage. A grid size of 5 km and a smoothing parameter of 185 km were chosen to account for geolocator error, and applied to all datasets in this comparison to control for differences in location error from each type of device (Merkel et al. 2016). I then compared observed vs. randomized overlap in core and general use area between stages for each week using Bhattacharyya's affinity (BA) and previously established methods (Breed et al. 2006; see Appendix S1.2 for details).

2. 2. 3 Mechanistic movement model

A two-parameter mechanistic model was used to investigate the potential drivers of juvenile and non-breeding adult movements (Revell & Somveille 2017). This model simulates the movements of a bird away from a given location and through a potential landscape defined by two environmental factors: (1) attraction to chlorophyll a concentration (a proxy for food resources; Grémillet et al. 2008) and (2) the effect of wind (i.e. assistance). Both variables were modelled as described in Revell and Somveille (2017) at a monthly and 0.25° resolution. Remotely-sensed chlorophyll data were obtained from NASA (https://neo.sci.gsfc.nasa.gov/view.php?datasetId=MY1DMM_CHLORA; Hu et al. 2012) and zonal and meridional wind speed components from NOAA (derived from up to 6 satellites - https://www.ncei.noaa.gov/thredds/catalog/uv/monthly/catalog.html; Zhang et al. 2006). These two datasets were averaged over the period from 2003 to 2015 to represent long-term conditions (i.e. a climatology) in the study area. I chose to use climatologies both to minimize gaps in measurements due to cloud cover, and because I hypothesize that differences in movement strategies of adults and juveniles are linked to longer-term (i.e. evolutionary) environmental processes (Woodward & Gregg 1998; Weimerskirch et al. 2000b; Suryan et al. 2012). As the NOAA dataset ends in 2011, the last four years (2011-2015) of monthly wind data were downloaded from Copernicus at the same spatial resolution for the two datasets (derived from SCATterometer [ASCAT] scatterometer onboard METOP-A and METOP-B satellites - WIND_GLO_WIND_L4_REP_OBSERVATIONS_012_003, https://resources.marine.copernicus.eu/; Bentamy & Fillon 2012). Wind speed and direction were compared between the NOAA and ASCAT datasets in years when both were available (2008-2011); differences were found to be minimal and did not influence model simulation outcomes (Appendix S1. 3). All environmental datasets were accessed in December 2019.

Within this potential landscape, the model framework assumes that birds are inherently attracted to resources, and I ran a range of scenarios varying the importance of the wind component relative to this attraction, characterized by the parameter *a*. Low values of *a* correspond to scenarios in which the effect of wind on movement patterns is minimal, and thus attraction to resources dominates, whereas progressively higher values of *a* reflect an increased role of wind on bird trajectories (Revell & Somveille 2017). An initial search of the parameter space of *a* revealed that there were no further variation in results below a=0.005 and above a=0.2, and I interpreted these extreme values as scenarios in which effects of resource attraction and wind-assisted movement dominated, respectively. Simulations were then run for values of *a* as multiples of 0.015 from 0.005 to 0.2, to investigate a broad range of scenarios (84 simulations in total). Another unknown parameter kT, representing the degree of randomness in the movement decisions, was set to a low value (0.05; Revell & Somveille 2017). All simulations began at Bird Island and were set to run for 3 months starting from April, the only month in which both non-breeding adults (6/16 birds) and juveniles (6/13 birds) departed from the colony in our study. Simulations were run 6 times for each value of *a* to capture the behaviour of both life-history stages.

The similarity between the resulting simulated and observed (the 6 juvenile and 6 non-breeding adults which departed the colony in April) tracks was investigated using Dynamic Time Warping (DTW), as this measure allows for the comparison of trajectories that may vary in time or speed (Ranacher & Tzavella 2014; Cleasby et al. 2019). Pair-wise DTW measures were computed for all tracks (simulated and observed), and the resulting distance matrix was examined using hierarchical clustering with a ‘ward-D2’ linkage, which minimizes within-cluster variance. Tracks were clustered to investigate which scenario of simulated tracks most closely aligned with observed adult and juvenile tracks using an increasing number of groups (k) ranging in value between 2 and 5, at which points the tracks

pertaining to a particular group (simulated, juvenile or non-breeding adult) were clustered separately.

2. 2. 4 Juvenile and non-breeding adult distributions and overlap with fisheries

I analysed overlap by week of the distribution of juveniles and non-breeding adults with longline fishing effort based on vessel movements to investigate potential difference in susceptibility to bycatch. Weekly core UDs were generated for each bird, resampled to a 0.1 x 0.1° resolution, and overlaid on a 0.1 x 0.1° grid of weekly fishing effort. Summed fishing effort per week for pelagic and demersal longline fisheries were collated from the Global Fishing Watch dataset (Global Fishing Watch [GFW] 2019, Option="drifting longline"). GFW provides information on daily fishing effort (hours) of vessels transmitting their location using an automatic identification system (AIS). As AIS is fitted to only 50-75% of active vessels that are over 24m in length (McCauley et al. 2016; Kroodsma et al. 2018; Shepperson et al. 2018; Sala et al. 2018), I determined whether the GFW dataset accurately captured longline fishing effort of all important fleets within the study area (South Atlantic Ocean) and period (April-July 2015) by contrasting the overlap of bird distributions with pelagic longline fishing effort using both AIS data (from GFW) and log-book effort data reported to the International Commission for the Conservation of Atlantic Tunas (ICCAT Task II Effort; https://www.iccat.int/en/accesingdb.html [Accessed April 2020]). As effort data from ICCAT were available at monthly, 5 x 5° resolution, monthly core UDs were generated for each bird for April and May (when sample sizes were high for juveniles), and re-sampled to a 5 x 5° resolution. Fishing intensity grids were obtained at the same spatial-temporal resolution for GFW data by summing 0.1 x 0.1 ° fishing effort (hours fishing) that fell within each 5 x 5° grid cell and daily effort for April and May of 2015 (Queiroz et al.

2019). Comparable effort data are not made available publically for demersal fleets operating within EEZs (see data availability statement; Clay et al. 2019).

Linear mixed-effect models were run to test for differences over time in overlap of juveniles and non-breeding adults with GFW fishing activity. The overlap score (hours.week^{-1}) was modelled as the response variable with individual ID as a random effect, and life-history stage (factor with two levels; non-breeding adult *NB*, and juvenile *JUV*), and weeks since departure from the colony (*Week*; factor with eight-levels; 1-8) were included as covariates. The Overlap score was square-root transformed to improve data spread. Model selection was conducted using the approach detailed in section 2.2.

Unless otherwise indicated, all means in the Results are given ± standard error (SE).

2. 3 Results

2. 3. 1 Distribution and movement characteristics of juveniles and adults

The juvenile white-chinned petrels fledged in April-May 2015 and dispersed in a northerly direction from South Georgia over a wide area in the South Atlantic Ocean (53.7°W-4.7°E). Individuals were tracked for periods of 1-57 days, with the last transmissions received by the ARGOS system in July 2015 (Fig. 2.1). The non-breeding adults tracked using geolocators began migration between late January and early May 2015, and spent the non-breeding period on the Patagonian Shelf and shelf-slope from Tierra Del Fuego to south-eastern Brazil, the western Argentine Basin, or the Humboldt Upwelling region off southern Chile. Adults tracked during incubation in December 2014 to January 2015 also travelled to the Patagonian Shelf, but foraged along the eastern coast of Argentina over what seems a more restricted area (the different accuracy of GPS and GLS data prevents a robust comparison) than that

used by non-breeding adults (Fig. 2.1 and see Tables S1.5 & S1.6 for complete tracking metadata).

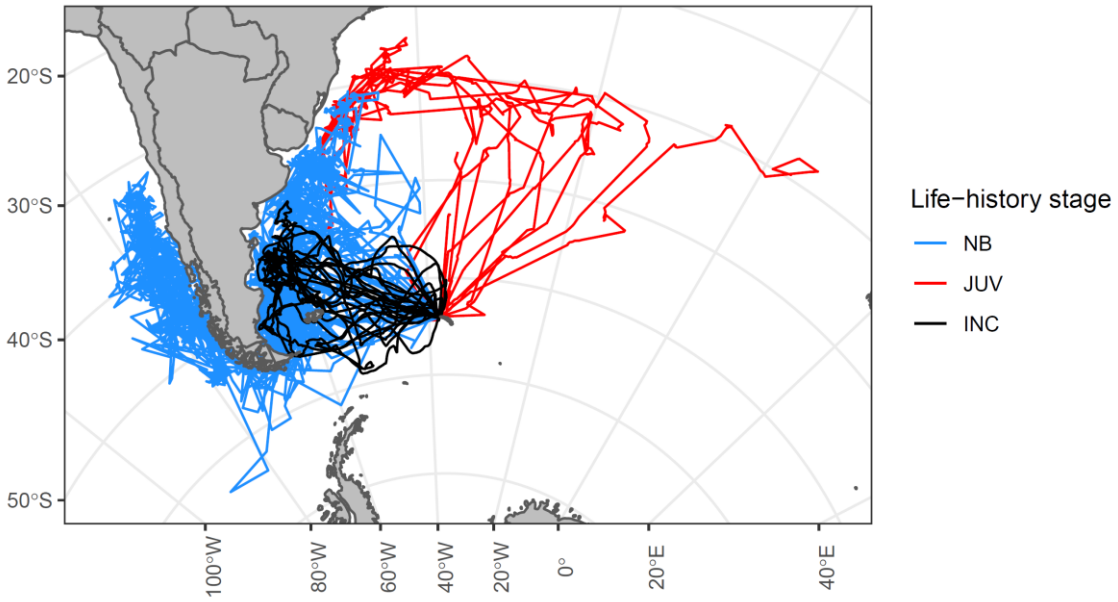

Figure 2. 1: Distribution of adult (incubating, INC; and non-breeding, NB) and juvenile (JUV) white-chinned petrels *Procellaria aequinoctialis* tracked from Bird Island (South Georgia) during the 2014/15 breeding season and subsequent winter. Incubating (n=12) and non-breeding (n=16) adults were tracked using Global Positioning System loggers (GPS) and Global Location Sensors (GLS), respectively, and juveniles (n=13) using Platform Terminal Transmitters (PTT).

Movement parameters of juvenile and non-breeding adults differed in the weeks following departure from the colony (Tables 2.1a and S1.7 for full model selection and Figures 2.2a and b); these differences (522 km maximum range and 20˚ longitude, on average) were far greater than would be expected just from location error associated with the different types of tracking device (~185 km for geolocators; Merkel et al. 2016). There was strong weekly variability in the maximum ranges reached by individuals of both stages (Fig. 2.2a), but overall maximum ranges increased during their first two weeks post-departure (Juveniles: 1457 ± 105 and 2772

± 118 km in weeks 1 and 2 respectively, Non-breeding adults: 935 ± 87 and 1618 ± 87 km in weeks 1 and 2 respectively) and then plateaued, after which further displacement away from the colony was minimal (< 82 km and <433 km per week for juveniles and non-breeders respectively). Average weekly longitudes also differed substantially between life-history stages; non-breeding adults travelled progressively west (reaching 64.2 ± 1.9° W in week 8) , whereas juveniles initially travelled east and only in their second week post-fledging changed direction to head progressively west towards the south American continent (to 47.4 ± 3.1° W in week 7, Fig. 2.2b). Both the core and general-use areas of the tracked juveniles differed significantly from those of non-breeding adults (Fig. 2.3 and Table 2.2), although there was some overlap from the fourth week onwards, as juveniles moved towards waters off southeast Brazil and Uruguay (Table 2.2).

Table 2. 1: Predictors retained in best supported linear mixed-effect models investigating differences in a) movement metrics of adult (non-breeding, NB and incubating, INC) and juvenile (JUV) white-chinned petrels *Procellaria aequinoctialis*, and b) overlap of the core distribution of NB and JUV birds with demersal and pelagic longline fishing effort. All birds were tracked from Bird Island (South Georgia) during the 2014/15 breeding season and subsequent winter. Models including all possible combinations of the predictor variables were considered, and ranked according to Akaike Information Criterion (AICc). Those reported below were within 2Δ of the best model. ''Life-history stages considered' indicates the life-history stages compared for a given movement metric; 'x' predictor variables retained in the best models; 'NA' variables that were not modelled; 'df' the degrees of freedom; 'Week' the weeks following departure from the colony; and 'AICcw' the AICc weight, the relative probability that a given model is the best model. See Table S1.7 for all combinations of predictors considered for model selection.

		Predictor variables							
Life-history stages considered	**Metrics**	Intercept	Life-history stage	Week	Life-history stage: Week	**df**	**AICc**	**ΔAICc**	**AICcw**
a) MOVEMENT METRICS									
NB vs. JUV	Maximum range (km)	x	x	x	x	18	2417	0.000	1.000
NB vs. JUV	Longitude (°)	x	x	x	x	18	1107	0.000	1.000
INC vs. JUV	Speed ($km.hr^{-1}$)	x	x	NA	NA	4	901.5	0.000	0.654
		x		NA	NA	3	902.8	1.272	0.346
INC vs. JUV	Sinuosity	x		NA	NA	3	2.082	0.000	0.857
JUV	Speed ($km.hr^{-1}$)	x	NA		NA	3	158.4	0.000	1.000
JUV	Sinuosity	x	NA		NA	3	-25.54	0.000	1.000
b) OVERLAP METRIC									
NB vs. JUV	Overlap score ($hours.week^{-1}$)	x	x	x	x	18	901.4	0.000	1.000

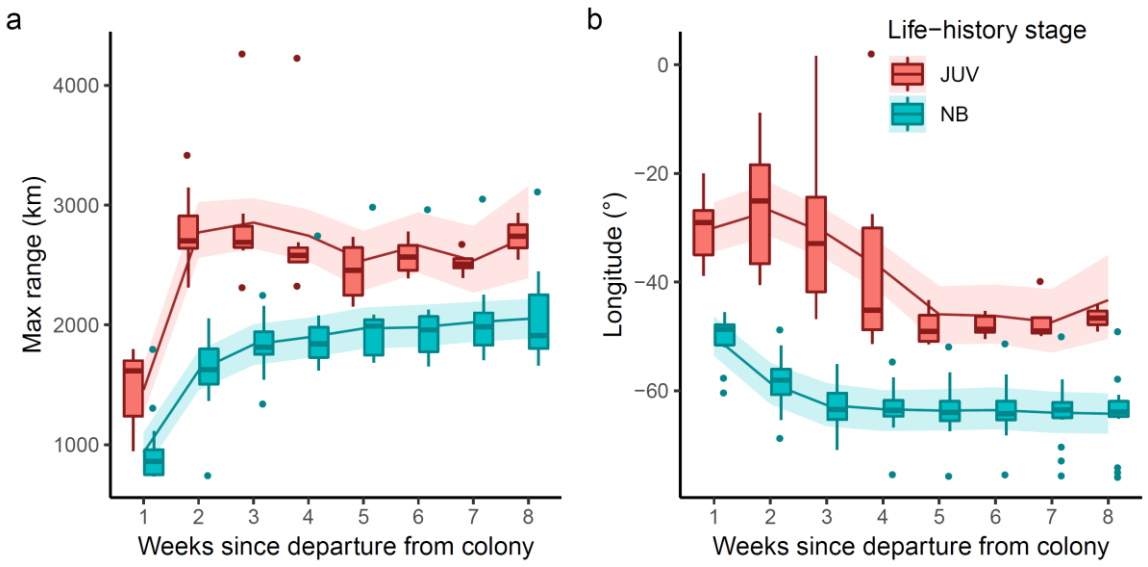

Figure 2. 2: Predicted average population values for (a) maximum range from the colony and (b) longitude using fitted linear mixed models for juvenile (JUV) and non-breeding adult (NB) white-chinned petrels *Procellaria aequinoctialis* in the first 8 weeks of departure from Bird Island (South Georgia) during the 2014/15 breeding season and subsequent winter. Lines and shading represent the model predictions and 95% confidence intervals for each life-history stage-week combination, respectively. Boxplots represent the spread of the observed data.

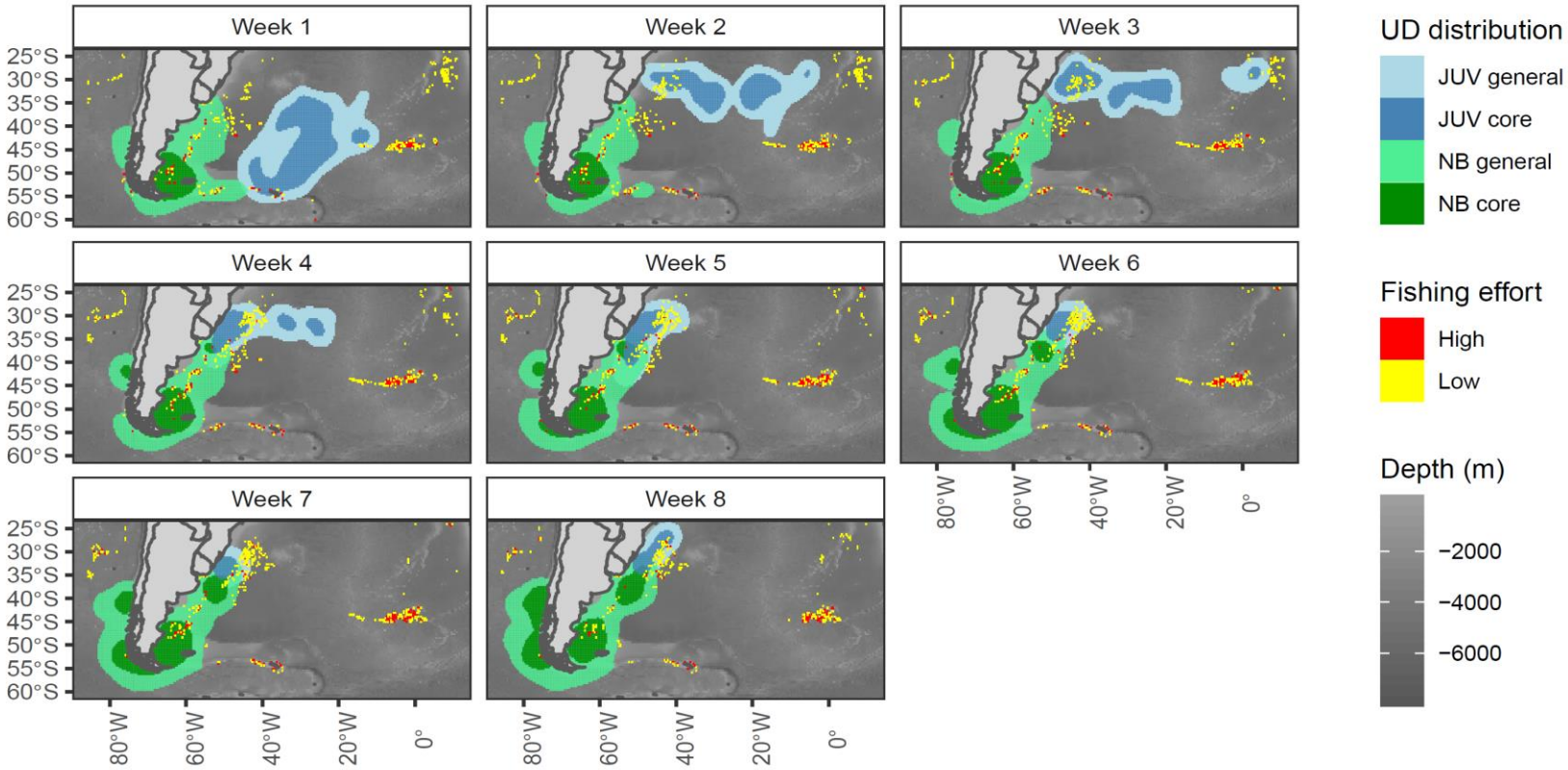

Figure 2. 3: Weekly core (61%) and general (95%) utilization distributions of temporally overlapping juvenile (JUV) and non-breeding adult (NB) white-chinned petrels *Procellaria aequinoctialis* in relation to pelagic and demersal longline fishing during the first eight weeks post-fledging from Bird Island (South Georgia). Birds were tracked from Bird Island during the 2014/15 breeding season and subsequent winter. High and low levels of fishing effort are here determined according to the 75% quantile of overall fishing effort (hours.week^{-1}); low effort< 6.8 hours.week^{-1} and high effort > 6.8 hours.week^{-1} based on the Global Fishing Watch (GFW) dataset.

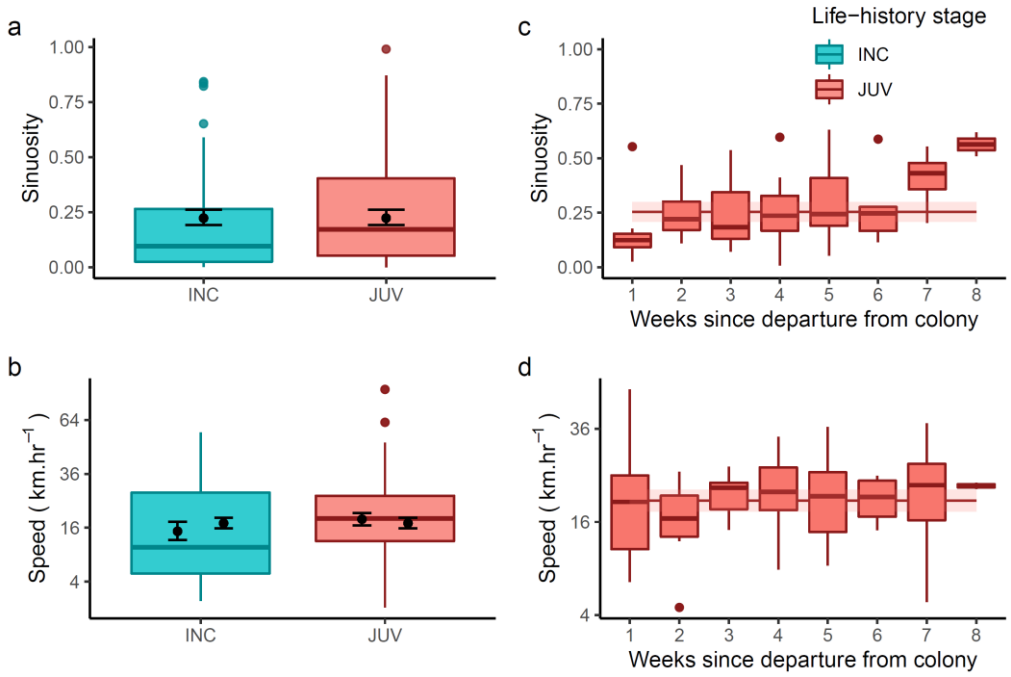

Figure 2. 4: (a-b) Predicted average population values for sinuosity and speed using fitted linear-mixed models for juveniles (JUV) and incubating adult (INC) white-chinned petrels *Procellaria aequinoctialis*. Dots and error bars represent the model predicted value and 95% confidence intervals for each life-history stage. Numbered dots and error bars in (b) represent the model predicted values and 95% confidence intervals for the top two models predicting speed. (c-d) Weekly predicted values are shown for juveniles only in the first 8 weeks of dispersal from their natal colony. Lines and shading represent the model predicted value and 95% confidence intervals for each week, respectively. Boxplots represent the spread of the observed data in all plots. Values of transformed response variables are back-transformed on the y-axis (b-d) but the scale of the transformation is retained.

Table 2. 2: Observed and randomized overlap (Bhattacharyya's affinity index) of utilization distributions (UD) between juvenile (JUV) and non-breeding adult (NB) white-chinned petrels *Procellaria aequinoctialis* tracked over the first 8 weeks since their departure from Bird Island (South Georgia) during the 2014/15 breeding season and subsequent winter. Randomized overlaps are shown as mean ± SD and P represents the proportion of randomized overlaps that were smaller than the observed.

Sample size			Core use area (61%)			General use area (95%)		
JUV	**NB**	**WEEK**	**Observed**	**Randomized**	**P**	**Observed**	**Randomized**	**P**
11	16	1	0.00	0.76 ± 0.06	**<0.001**	0.00	0.73 ± 0.06	**<0.001**
8	16	2	0.00	0.76 ± 0.08	**<0.001**	0.00	0.71 ± 0.07	**<0.001**
8	16	3	0.00	0.76 ± 0.10	**<0.001**	0.00	0.71 ± 0.07	**<0.001**
8	16	4	0.01	0.71 ± 0.12	**0.001**	0.10	0.77 ± 0.09	**<0.001**
7	16	5	0.08	0.64 ± 0.13	**<0.001**	0.22	0.77 ± 0.09	**<0.001**
6	16	6	0.00	0.54 ± 0.16	**<0.001**	0.09	0.72 ± 0.10	**<0.001**
4	16	7	0.03	0.43 ± 0.24	**0.012**	0.21	0.65 ± 0.13	**<0.001**
2	16	8	0.04	0.27 ± 0.22	**0.037**	0.13	0.48 ± 0.14	**<0.001**

2. 3. 2 Mechanistic movement model

Hierarchical clustering of pair-wise DTW distances provided strong evidence that, when compared to the simulated tracks, the observed tracks of juveniles were strongly influenced by wind, whereas those of non-breeding adults were influenced to a much greater extent by attraction to resources (see full hierarchical clustering results in Fig. S1.4). Initially, the

analysis grouped 60 simulated tracks into one cluster, and 24 simulated tracks and all observed tracks (6 juvenile and 6 non-breeding adults) into a second cluster (k=2). Increasing k to 3, however, separated the second cluster into two more groups; the first (Cluster 2; Fig. 2.5d) containing all observed juvenile tracks and 18 simulated tracks, and the second (Cluster 2.3; Fig. 2.5d) containing all observed non-breeding adult tracks and 6 simulated tracks. Increasing the number of clusters first separated all but one of the non-breeding adult tracks from the simulated tracks with a low a value (k=4), and then the juvenile tracks from the simulated tracks with a high a value (k=5).

For k=3, all simulated tracks from Cluster 2 corresponded to simulations run with higher values of a (0.11-0.2), suggesting that the routes taken by the tracked juveniles were strongly influenced by prevailing wind speed and direction in the south Atlantic Ocean (Fig. 2.5b). Indeed, simulated and observed tracks in Cluster 2 indicated that routes of white-chinned petrels departing from South Georgia followed the prevailing westerly winds in a north-easterly direction until birds reached 30°S. North of 30°S, the prevailing winds are easterlies, and the birds changed direction accordingly, travelling west until they reached the nearest productivity hotspot located off the coast of Uruguay and southeast Brazil.

For k=3, all simulated tracks in Cluster 3 corresponded to simulations run with the lowest a value possible (0.005), suggesting that dispersal patterns of non-breeding adults from the colony were driven by attraction to resources (Fig. 2.5c). Simulated and observed birds from Cluster 3 followed slightly different trajectories, but they both dispersed towards the Patagonian Shelf. This is the closest area to South Georgia with consistently high chlorophyll concentrations, particularly during the austral winter. Adults travelled into, rather than with the prevailing westerly winds to reach this region.

Finally, for *k*=3, all tracks grouped within Cluster 1 corresponded to simulations run with intermediate values of *a* (0.02-0.185; Fig. 2.5d), equating to a scenario in which movements are moderately influenced by wind relative to the attraction to resources. Simulated tracks were in a north-easterly direction until 30-45°S, at which point they turned directly east towards the productivity hotspot located off the coast of Namibia (Fig. 2.5a). It is worth noting that one juvenile which departed from the colony in May also headed in this direction before the transmitter ran out, suggesting that heading towards the African coast may be a rare strategy conducted by a minority of individuals. Two simulated tracks went west instead, but towards more northerly locations along the South American coast, which would explain why they did not group into Cluster 2 for *k*=3.

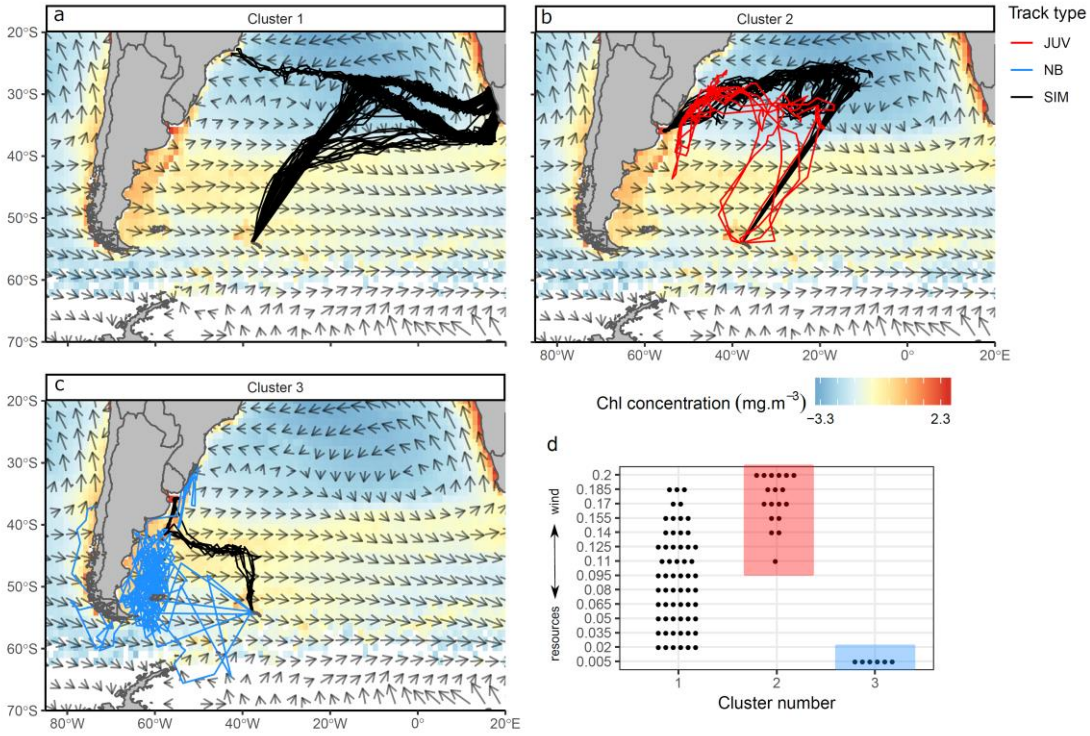

Figure 2. 5: (a-c) Hierarchical clustering of observed (JUV= Juvenile, NB=Non-breeding adults) and model-simulated (SIM) tracks in relation to chlorophyll concentration and wind speed and direction. Results are shown for clustering of tracks into three groups (*k*=3). Birds were tracked from Bird Island (South Georgia) in the 2014/15 breeding season and subsequent winter. Wind direction and speed are represented by the direction and length of arrows, respectively, and chlorophyll concentration is log transformed. (d) The number of simulated tracks (represented by black dots) present in each cluster for a given value of *a*, and red and blue shaded boxes highlight the groups in which simulated tracks clustered with observed juvenile and non-breeding adult tracks, respectively.

2. 3. 3 Spatial overlap with longline fishing vessel activity

As a result of differences in their at-sea distributions, non-breeding adults and juveniles varied in the location and extent of their overlap with demersal and pelagic longline fishing activity (Figures 2.3, 2.6 & 2.7 and Tables 2.1b and S1.7 for full model selection). On average, there was less longline fishing activity (by c. 130 hours, from vessels with active AIS) in the 0.1 x 0.1° grid cells used by juveniles than those used by non-breeding adults (Fig. 2.6a), mainly because juveniles spent the first few weeks post-fledging in areas of the south Atlantic Ocean where few vessels operate (Fig. 2.3). Although overlap scores were lower for juveniles, they nevertheless overlapped with fishing vessels with active AIS from the first week after fledging from South Georgia. In addition, average scores increased over the study period, from a low of 0.03 hours in week 2, to a high of 9.55 hours in week 8, as individuals reached the coastal waters of Uruguay and southeast Brazil (Figures 2.3 & 2.6). In this region however, there are likely to be a large proportion of vessels operating without active AIS, as coarser-scale analyses using ICCAT effort data revealed substantial overlap of juveniles with the fleets of Taiwan and Brazil, while overlap was negligible using GFW effort data (Fig. 2.7).

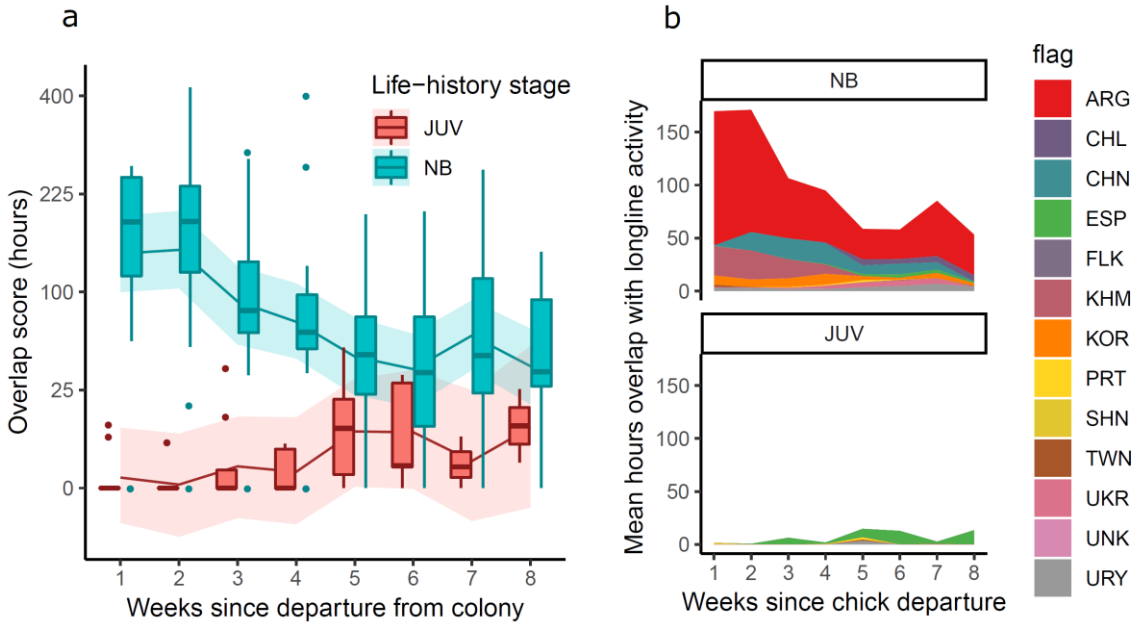

Figure 2. 6: (a) Predicted average population values for overlap scores of the core use areas of juvenile (JUV) and non-breeding (NB) adult white-chinned petrels *Procellaria aequinoctialis* with pelagic and demersal longline fishing activity (obtained from Global Fishing Watch) using fitted linear-mixed models over the first 8 weeks of the dispersal of juveniles from their natal colony, and the average corresponding temporal distribution for non-breeding adults. Lines and shading represent the model predicted value and 95% confidence intervals for each stage-week combination, respectively. Boxplots represent the spread of the observed data. (b) Mean fleet-specific overlap. ARG = Argentina, CHL= Chile, CHN = China, ESP = Spain, FLK = Falkland Islands, KHM = Cambodia, KOR = South Korea, PRT = Portugal, SHN = Saint Helena, TWN = Taiwan, UKR = Ukraine, UNK = Unknown, and URY = Uruguay.

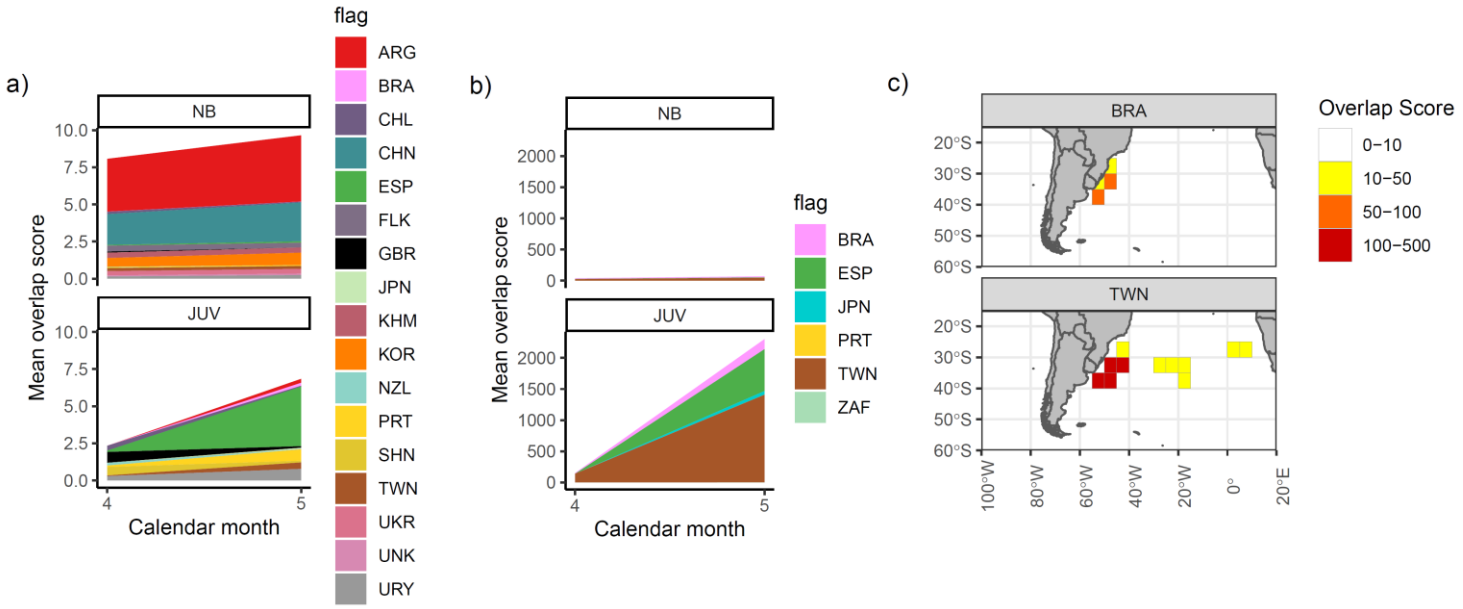

Figure 2. 7: Mean individual overlap of the core use areas of juvenile (JUV) and non-breeding adult (NB) white-chinned petrels *Procellaria aequinoctialis* tracked from Bird Island (South Georgia) in the 2014/15 breeding season and subsequent winter with a) longline effort (pelagic and demersal) as recorded in the Global Fishing Watch dataset (overlap score = hours.10^3), and b) pelagic longline effort as reported to ICCAT (overlap score = hooks.10^3) for April and May 2015 (Calendar months 4 and 5, respectively). (c) Overlap of the core use areas of juvenile white-chinned petrels with Brazilian and Taiwanese pelagic longline effort as reported to ICCAT in May 2015. Overlap score = hooks.10^3. ARG = Argentina, BRA=Brazil, CHL= Chile, CHN = China, ESP = Spain, FLK = Falkland Islands, GBR = Great Britain, JPN = Japan, KHM = Cambodia, KOR = South Korea, NZL = New Zealand, PRT = Portugal, SHN = Saint Helena, TWN = Taiwan, UKR = Ukraine, UNK = Unknown, and URY = Uruguay.

The main areas of fisheries overlap were around South Georgia, along the coast from Argentina to southeast Brazil, around Tristan da Cunha, and off Namibia (Figures 2.3 & 2.7). Overlap of juveniles with longline vessels fitted with AIS was dominated by Spain (weeks 2-4 and 6-8), and, to lesser extents, Uruguay, Portugal, St. Helena and Ascension Islands and Taiwan (Fig. 2.6b). Overlap with Taiwan may be underestimated however, particularly in May, as revealed by the coarser-scale analysis of log-book data reported to ICCAT (Fig. 2.7). Individuals also overlapped with Brazilian fleets in the same month, but to a lesser extent (Fig. 2.7). Non-breeding adults overlapped more with longline fishing vessels with active AIS because they migrated to the productive Patagonian Shelf, where fishing activity was much more concentrated (Fig. 2.3). Overlap was high from Tierra Del Fuego to southeast Brazil, and dominated by the fleets of Argentina (weeks 1-8), followed by Cambodia, China, South Korea, and, to a lesser extent, Uruguay, Chile, Ukraine, Spain, Taiwan, Portugal and the Falkland Islands (Fig. 2.6b).

2. 4 Discussion

Through combining individual tracking data and a mechanistic model, I found that juveniles and adults differed in their movement patterns and that movements were best explained by different processes: wind-assisted movement in juveniles, and attraction to productive regions, irrespective of wind conditions, in adults. While our study used tracking devices with different degrees of spatial error, by re-sampling locations to the same interval and smoothing spatial distributions to the same extent, I am confident the results represent true differences in behaviour between life-history stages. These results provide considerable insight into the ontogeny of movement strategies in the context of learned versus innate behaviour. Moreover, the divergent movement patterns of adults and juveniles have important implications for the conservation of this threatened seabird species.

2. 4. 1 Ontogeny of movement strategies: learned vs. innate behaviour

The capacity for long-distance movement is widespread in the animal kingdom, and movement strategies are commonly thought to develop through a combination of learning (social or individual) or genetic programming in young life-history stages (Weinrich 2008; Putman et al. 2014). In many species of birds (terrestrial and marine), young individuals may follow one or both of their parents on their first foraging flight or migration, allowing them to learn a migration route and the location of feeding areas, or to develop their foraging skills (Regehr et al. 2001; Harding et al. 2004; Guo et al. 2010). In contrast, juvenile white-chinned petrels fledge independently from their parents and, as our study showed, rapidly flew large distances from the colony. Remarkably, their flight speeds and sinuosity were similar to those of breeding adults, suggesting comparable flight capability. Young individuals of other petrel and albatross species also disperse rapidly away from their natal colony, suggesting an innate ability to orient with respect to wind direction, and fly with a high level of efficiency immediately after fledging (Alderman et al. 2010; Riotte-Lambert & Weimerskirch 2013; de Grissac et al. 2016). This is not typical of other seabird taxa, however, which instead show progressive improvements in their flight performance with the number of days since fledging (Yoda et al. 2004; Mendez et al. 2019; Corbeau et al. 2019).

Navigating across the seemingly featureless pelagic ocean seems challenging, but innate flight skills may allow juveniles to search for patchily-distributed resources across large spatial scales, similarly to adults (Adams et al. 1986; Warham 1990; Weimerskirch et al. 2000b; Alerstam et al. 2003). Indeed, when the juvenile tracks were compared to model simulations, the best match was with environmental scenarios dominated by wind, suggesting movements of juveniles are strongly influenced by prevailing wind patterns in the South Atlantic. As the model assumes some inherent attraction to resources (Revell & Somveille 2017), even for wind-dominated scenarios, I was unable to simulate a scenario whereby there

was full passive drift (like sea turtles with ocean currents; e.g. Scott et al., 2014). However, as prevailing winds at 40-60°S are westerly, I presume that under a full-drift scenario, birds would be carried eastwards such that they would very likely arrive in the Indian Ocean. None of the tracked birds did this, but instead made directed movements northwards for >2000 km before, for the most part, following trade winds westwards. While the cues used by juvenile seabirds to navigate are poorly known, I suggest that this initial direction is highly likely to be innate as it was followed by all our tracked juveniles. The same mechanism likely explains the initial bearings of juvenile white-chinned petrels, Indian yellow-nosed albatrosses *Thalassarche carteri* and black-browed albatrosses *T. melanophris* fledged from Kerguelen, Amsterdam or Crozet Islands, which make directed movements towards the productive coasts of South Africa or Australia (de Grissac et al. 2016). Ultimately, as juveniles in our study eventually reached a productive hotspot off the coast of Uruguay and southeast Brazil after several weeks of travel, wind-assisted movement may thus represent a low-energy strategy that minimises costs of searching for prey if lacking prior knowledge of the environment.

Juveniles travelled along different routes to migrating adults; indeed, the routes taken by tracked adults towards the productive South American coast best matched resource-dominated scenarios, indicating that they migrate directly towards productive foraging habitats (Phillips et al. 2006), based on prior knowledge of their environment (memory). In contrast, juveniles initially travelled across less productive waters in the first few weeks post-fledging, which presumably reduces competition with older birds while they refine their foraging skills (similar to northern and southern giant petrels, *Macronectes halli* and *M. giganteus*; Thiers et al. 2014; de Grissac et al. 2016). Although the tracking period only lasted eight weeks, the juvenile white-chinned petrels eventually reached a foraging area on the Patagonian Shelf just north of that used by nonbreeding adults, and presumably move progressively south into the latter over the following months or years. A similar ontogenetic

shift in habitat use, often associated with changes in morphology, energetic demands or competitive abilities has been recorded in a wide range of taxa, including seabirds, and may have far-reaching consequences in terms of the mortality risk of different age classes (Garcia-Berthou 1999; Field et al. 2005; Phillips et al. 2017). Adult seabirds typically show very high fidelity to their main nonbreeding areas, even if individuals show smaller-scale differences in migration routes, staging areas etc. from year to year (Phillips et al. 2017). Hence, the juvenile phase seems to be critical in the development of a migration strategy that in most oceanic seabirds will persist through their life.

Finally, while the environmental variables considered here (particularly wind) vary substantially over small temporal scales (Rivas et al. 2006; Desbiolles et al. 2017), simulated tracks generated using 12-year averages of resource availability and wind components matched observed tracks closely. This suggests that birds track environmental processes over longer time-periods (both as a result of memory and innate mechanisms). Over the last decade, there has been little variation between years in ocean winds (Marcos et al. 2019); however, westerlies are gradually strengthening and shifting poleward, which may affect initial juvenile dispersal in the future (Toggweiler 2009). As for productivity, chlorophyll a concentration has generally increased over the Patagonian Shelf, presumably increasing attraction to this region associated with higher resource availability (Dunstan et al. 2018).

2. 4. 2 Consequences of movement patterns for overlap with threats at sea

The white-chinned petrel is one of the most common bycaught seabirds in longline fisheries, because they are numerous, compete aggressively for bait, offal and discards, can dive to >10 m, and occur in productive shelf habitats where fisheries are often concentrated (Cherel et al. 1996; Barnes et al. 1997; Weimerskirch et al. 1999). Adults from South Georgia winter on the Patagonian Shelf and off southern Chile, both areas of high demersal and pelagic longline

fishing effort (Phillips et al., 2006). Overlap of core-use areas of non-breeding adults with longline fishing activity (based on satellite AIS data) was therefore predictably high in our study, and many of the fleets have previously reported bycatch of white-chinned petrels (Argentina, Taiwan, Uruguay and Chile; Moreno et al. 2006a; Jiménez et al. 2009; Favero et al. 2013; Yeh et al. 2013), suggesting a good correspondence between overlap and bycatch rates. Our analysis did not indicate overlap between the non-breeding adults and Brazilian longline fleets – which have reported bycatch of white-chinned petrels (Bugoni et al. 2008), probably because many of those vessels are not fitted with AIS transponders, indicating a current limitation of the Global Fishing Watch dataset. Overlap with this fleet was also low when using effort data available from ICCAT, underlining potential gaps in reporting to RFMOs at a regional level. However, I revealed some overlap with longline vessels from Cambodia, China and South Korea, from which there are no published reports of seabird bycatch. Overlap indices are scale-dependent and by studying overlap at fine spatial and temporal scales, our study highlighted new fleets for which bycatch may be a major concern, emphasizing the pressing need for much more comprehensive monitoring of seabird bycatch rates and uptake of mitigation (Phillips, 2013; Torres et al., 2013).

In contrast to adults, juveniles overlapped to a lesser extent with longline vessels fitted with active AIS. A low level of overlap occurred from the first week from fledging, however, it then increased over the following months as juveniles shifted distribution west towards the coast of South America. This has important implications for the dynamics and potential recovery of this threatened population. The naïve behaviour of juvenile seabirds is considered to render them more susceptible to bycatch than more experienced adult life-stages (Gianuca et al. 2017). For the first two months, the juvenile white-chinned petrels mostly overlapped with pelagic longline fleets from a variety of flag states operating under the jurisdiction of ICCAT; south of 25°S, these are required to use at least two of three

mitigation measures: night setting, bird-scaring (Tori or streamer) lines and line weighting (ICCAT 2009; Gilman 2011). However, 95% of these vessels lack independent monitoring, observer coverage is poor, and, as a result, these measures are not implemented consistently (Gilman 2011; Brothers & Robertson 2019). It is thus likely that incidental mortality of juveniles occurs, which may be a major contributing factor to the population decline recorded at South Georgia (Berrow et al. 2000a).

2. 4. 3 Conclusion

Here I demonstrated that a mechanistic movement model can be used to better understand the environmental drivers of divergent movement strategies within seabird populations. Moreover, due to their focus on underlying processes, mechanistic frameworks offer promising applications for predicting how individuals may be exposed to and respond to changes in their environment (Leroux et al. 2013; Bocedi et al. 2014; Evans et al. 2019). It is also important that scientists continue tracking individuals across life-history stages to understand variation in the drivers of habitat use among and within species, and any consequences for susceptibility of each age class to different threats (Hazen et al. 2012; Afan et al. 2019; Clay et al. 2019; Carneiro et al. 2020). In the context of mitigating fisheries bycatch in seabirds, the development of exciting new bio-logging tools (for example loggers which detect fishing boat radar; Weimerskirch et al. 2018) are paving the way for an increased understanding of marine predator-fisheries interactions at fine spatial-temporal scales, and will be crucial in setting future management priorities.

CHAPTER 3 – The ontogeny of movements and habitat selection in juvenile albatrosses revealed through integrative step selection analysis

This chapter is in preparation for publication, and will be co-authored by Manica A., Clay T. A., Wood A. G. and Phillips, R. A.

Author contributions:

I conceived the project, developed the research questions, conducted the data analysis and wrote up the chapter with supervision from R. A. Phillips & A. Manica.

T. A. Clay provided assistance with selection of environmental data, model formulation (and hypotheses to test) and feedback on the first version of the manuscript.

A. G. Wood managed tracking data download and storage, and will provide feedback on future versions of this manuscript.

ABSTRACT

Optimal selection of foraging habitat is key to survival, but it remains unclear how naïve individuals are able to locate and access resource patches in completely new environments. In many animals, dispersing juveniles receive no parental guidance and hence external cues may play an important role in guiding movements; however, it remains challenging to pinpoint when and how individuals learn to exploit their local environment, especially in species with cryptic life-stages. Here, I use a mechanistic modelling framework - integrated step selection analysis - to examine the development of habitat preferences in a oceanic seabird with a prolonged period of immaturity, the grey-headed albatross (*Thalassarche chrysostoma*). Juveniles were tracked from Bird Island, South Georgia, over two years (n = 9 in 2018 and n = 14 in 2019), using satellite transmitters (Platform Terminal Transmitters or PTTs), and I investigated ontogenetic changes in individual movement characteristics (step lengths and turning angles) in response to two environmental variables; winds (a low-cost driver of movement) and chlorophyll a concentration (a proxy for resources) during their first four months at sea. Naïve juveniles dispersed rapidly away from South Georgia using winds to increase travel speeds and orient towards a common destination (subantarctic and subtropical waters in the east Atlantic Ocean). Birds also responded to resource availability immediately after fledging by reducing their travel speeds in productive regions, but showed a marked progression in their large-scale movement patterns, thereafter engaging in slow and progressively more sinuous movements from their second month onwards. While more complex movement strategies such as return migrations take longer to develop in this wide-ranging bird, my results suggest that juveniles are rapidly able to respond to changes in wind for efficient flight and forage in association with areas of high productivity.

3. 1 Introduction

Habitat selection is the decision-making process through which animals choose resources relative to their availability or accessibility (Johnson 1980). While the location of certain high-quality habitats may be predictable, food items are often patchily distributed in time and space, and a number of extrinsic and intrinsic processes (e. g. competition, predation and breeding constraints) may limit access to productive areas (Stephens & Krebs 1986; Fauchald 1999; Piatt et al. 2006). Making optimal decisions about which habitats to target and how to access these patches thus constitutes a complex process, requiring individuals to recognize food, memorize profitable areas, reduce travel costs, fine-tune their behaviour to fluctuating conditions and potentially seek out new foraging habitats in order to meet their energetic requirements (Rebach 1996; Merkle et al. 2019; Beumer et al. 2020; Villard & Taylor 1994). These abilities are expected to give rise to specific habitat preferences and movement strategies (e. g. migratory routes) that maximize individual fitness, yet it remains unclear how these vital skills develop in naïve individuals with no prior experience of their environment (Hazen et al. 2012; Kays et al. 2015; Pyke 2019).

In animals with parental care, juveniles undergo a transition from dependence on delivered food to independent feeding (Guo et al. 2010; Riotte-Lambert & Weimerskirch 2013). Mortality is often high during this period as young individuals typically have lower foraging efficiency than adults because of inexperience and physical immaturity (Lack 1954; Ashmole 1963; Daunt et al. 2007a). Young of some species benefit from extended parental support (e. g. primates, boobies and tropical passerines; Rapaport & Brown 2008; Guo et al. 2010; Tarwater & Brawn 2010), but in others (e. g. sea turtles, procellariform seabirds and some pinnipeds; Shillinger et al. 2012b; de Grissac et al. 2016; Orgeret et al. 2019), they are abandoned at their natal sites and must acquire food in an unknown environment with no such guidance. In these instances, skills that are necessary for finding food may be

genetically determined, such as the ability to navigate or to move efficiently by exploiting favourable winds (Vega et al. 2016; Chapter 2). However, it is likely that individuals also undergo a period of learning and adjustment to their environment during which external cues (e. g. physical, chemical, biological and social) play an important role in shaping initial movements (Campagna et al. 2006; Watts 1985; Kennedy & Ward 2003; Vila Pouca et al. 2020).

Quantifying the relationship between environmental conditions and early-life behaviour can be challenging as juveniles have low survival rates, may be smaller than adults and disperse to remote areas, making them difficult to observe for long periods of time (Hazen et al. 2012; Kays et al. 2015). In particular, within marine environments, juveniles of many species seemingly 'disappear' for many years before returning to their natal grounds to breed, but developments in tracking technology (miniaturisation and increasing battery life) are progressively uncovering the movements of these cryptic life-stages (Shillinger et al. 2012a; Péron & Grémillet 2013; Mansfield et al. 2014). These studies have mainly focused on using movement data to determine age-specific habitat associations, rather than the mechanisms underpinning individual movement decisions (Andersen et al. 2013; Ketchum et al. 2013; Gutowsky et al. 2014). However, analytical frameworks which model animal movement as a series of discrete steps, characterised by specific velocity and autocorrelation distributions, are becoming more accessible, providing useful tools for identifying the key extrinsic features that drive observed movement patterns (Breed et al. 2018; Carter et al. 2020; Biddlecombe et al. 2020). In particular, integrated step-selection functions seem well-suited for investigating how strategies develop over time as they allow the user to investigate different movement processes concurrently, for instance cues aiding travelling (e. g. ocean and wind currents; Nourani et al. 2018) vs. foraging behaviour (e. g. oceanography and prey

availability; Roberts et al. 2021), whilst also accounting for accessibility (i. e. the potential environment an individual could have sampled at each step) (Avgar et al. 2016).

Oceanic seabirds dispersing at sea after fledging represent fascinating study systems for researching ontogenetic changes in movements and habitat selection, as they have prolonged immaturity stages during which naïve individuals must learn to navigate a seemingly featureless ocean in search of sparse prey patches (MacLean 1986; Shaffer et al. 2006; Weimerskirch et al. 2014). Adults are reliant on winds to cover great distances at low energetic cost (Weimerskirch et al. 2000b) and generally switch from fast and directed movement (indicative of travelling) to slow and sinuous movement (indicative of searching or foraging) in response to both static topographic (e.g. continental shelf-break; Freeman et al. 2010) and dynamic oceanographic features (e.g. mesoscale fronts, eddies; Dean et al. 2013; Scales et al. 2016) which are known to concentrate prey. Tracking studies have shown that juveniles are similarly capable of very large-scale movements post-fledging and that they show a tendency to switch to more sinuous exploratory movements over time (Alderman et al. 2010; de Grissac et al. 2016; Corbeau et al. 2019). However, as many of these investigations make broad level, qualitative descriptions of changes in behaviour, little is known of the processes responsible for generating these patterns. Understanding which cues juveniles use and how they respond to these in order to optimize movements and selection of foraging habitat may help shed light on how naïve individuals survive the critical learning period; which is of key ecological and conservation value given these life-stage can make up to 50% of populations (Weimerskirch et al. 1997a; Saether & Bakke 2000; Pardo et al. 2017).

Here I use integrated step-selection analysis to investigate these ontogenetic processes in a very long-lived and wide-ranging seabird, the grey-headed albatross (*Thalassarche chrysostoma*). Specifically, I analysed movement data from juveniles tracked after fledging from Bird Island, South Georgia, in 2018 and 2019 with the aims of (a) describing general

post-fledging movements, and (b) quantifying whether individuals showed a progression in their movement characteristics (step lengths and turning angles) during their first four months at sea, and c) how birds respond to local environmental conditions, specifically winds (a driver of low-cost movement) and chlorophyll a concentration (a proxy for prey availability; Grémillet et al. 2008), and d) whether movement responses to environmental cues changed over time. Given naïve individuals have no prior experience of their environment, I hypothesize that juveniles will disperse away from their colony using a low-cost route, i.e., by using prevailing winds. I thus expected wind speeds to increase juvenile displacement rate and directional persistence. Secondly, as individuals develop their foraging skills or encounter favourable habitats over time, I hypothesize that resources will play an increasingly important role in determining how juveniles move irrespective of wind conditions, i.e., that there would be inverse relationships between displacement rate, directional persistence, and chlorophyll a concentration.

3. 2 Materials & Methods

3. 2. 1 Deployments and tracking data processing

Juvenile grey-headed albatrosses were tracked after fledging from Bird Island, South Georgia (54°00'S, 38°03'W), in May-June 2018 (n=9) and 2019 (n=14) using Telonics TAV-2630 satellite transmitters (Platform Terminal Transmitters, PTTs) with a duty cycle of 8-hr ON and 48-hr OFF for 101.1 ± 47.5 and 82.7 ± 54.3 days on average in 2018 and 2019 respectively (for details see Chapter 4). PTTs were attached to the back feathers using Tesa© tape and provided locations every 40 minutes on average during ON periods. In all cases, the total mass of devices including tape used for attachment (40 g) was less than the 3% threshold of body mass beyond which deleterious effects are more common in oceanic seabirds (Phillips et al. 2003). All locations from PTTs in ARGOS classes A, B, 0, 1 and 3 were used, but unrealistic positions requiring a sustained flight speed of over 90 $km.h^{-1}$ were

removed (McConnell et al. 1992). Only ON periods were considered for analysis, and therefore remaining data were interpolated at 40 minute intervals within ON periods to obtain regular positions, and ON periods with fewer than three locations were removed from subsequent analysis to enable the calculation of turning angles (see below 2.2).

3. 2. 2 Integrated step-selection models

I used integrated step-selection analysis (*i*SSA; Avgar et al. 2016) to investigate the ontogeny of foraging behavior in juveniles. This modelling framework is ideal for investigating the processes influencing naïve movement decisions, as it can test for responses to external conditions encountered *en route*, thereby approximating a juvenile exploring its environment for the first time, rather than test for selection of specific habitats (e. g. Clay et al. 2016), which assumes prior knowledge of the accessible area. Indeed, consecutive movements are represented by a fixed time step length and turning angle (the distance and change in travel direction between consecutive locations, respectively). In addition, environmental covariates can be extracted at the start of individual steps and included in the *i*SSA as an interaction with movement characteristics (step length and turning angle) to test whether they have a significant effect on the response of individuals to local conditions by comparing observed step characteristics with those of 'possible steps' randomly sampled from analytical distributions fitted to all observed step lengths and turning angles (see description of step randomization below). Here, I computed steps lengths and turning angles from the tracking data using the 'amt' package (Signer et al. 2019), and investigated the response of individuals to two environmental variables ; a) chlorophyll a concentration (a proxy for prey resources), and b) winds (a proxy for the cost of movement; Wakefield et al. 2009b). Although grey-headed albatrosses are known to forage in association with a number of oceanographic features (e. g. oceanic fronts and eddies; Clay et al. 2016; Scales et al. 2016), I chose to

include one holistic indicator of productivity to avoid over-parameterizing the model which includes three-way interactions (see full model structure below).

Monthly remotely-sensed chlorophyll data ('chl') were obtained from the GlobColour-merged chlorophyll *a* product disseminated via the Copernicus Marine Environmental Monitoring Service (https://resources.marine.copernicus.eu/?option=com_csw&view=details&product_id=OCEANCOLOUR_GLO_CHL_L4_REP_OBSERVATIONS_009_082; accessed June 2020; Garnesson et al. 2019). Wind speeds ('wind') were computed from hourly zonal and meridional wind speed components downloaded from the European Centre for Medium Range Weather Forecasts (ECMWF) ERA5 reanalysis dataset (https://doi.org/10.24381/cds.adbb2d47; accessed June 2020). As data are available at 10 m above sea level yet mean recorded flight heights for grey-headed albatrosses are around 3.5 m, wind speeds were reduced to this height using a logarithmic model of wind gradient (assuming a scale height of 0.03 m; Pennycuick 1982b; Wakefield et al. 2009b). Both environmental variables were available at a 0.25° spatial resolution, corresponding to around 15-25 km given the latitudes used by tracked birds, and were projected using a Lambert azimuthal equal-area projection centered at 90°S and 38°W to limit distortion. Mean covariate values at each tracking location were extracted using a 1.5 km buffer with the function 'gBuffer' in package 'raster' (Hijmans et al. 2010) to account for PTT location error (CLS Argos 2008), and standardized using the function 'scale' available within base R.

In order to determine how movement in response to environmental variables changed over time, I included the calendar month since fledging ('month') as a factor interacting with step lengths, turning angles and environmental covariates in four three-way interactions; (1) month * step * wind, (2) month * step * chl, (3) month * turn * wind and (4) month * turn * chl. As the sample size of tracked individuals reduced in number over time due to device failure, I applied the *i*SSA to the movement data from the first four post-fledging months only

(Table S2. 1). Juveniles tracked in 2018 and 2019 did not differ significantly in terms of their step-length distribution and only to a small extent in terms of turning-angle distribution (yearly means differed by ~ 0.02 radians), and were therefore pooled to increase monthly sample sizes (Table S2. 2 and Figures S2. 2a & b). Furthermore, step lengths of birds were much shorter during darkness than daylight (9.1 ± 12.1 vs 23.7 ± 18.1 $km.hr^{-1}$) suggesting that juveniles rarely travel or search for prey during darkness (Table S2. 2, Figures S2. 2 c & d and in line with de Grissac et al. 2017; Pajot et al. 2021), and hence steps occurring during the night were excluded from the *i*SSA.

I fitted a Gamma distribution to the remaining observed step lengths of all individuals (n = 2498 total steps; n = 859 in month 1, n = 637 in month n = 2, 566 in month 3 and n = 436 in month 4) and a Von Mises distribution to the turning angles using the 'amt' package (Signer et al. 2019). A set of models fitted using conditional logistic regression (function "clogit" in the R package "survival"; Therneau 2015) and consisting of all observed steps and varying numbers of random steps (up to 100) found that coefficients for each parameter and model cross-validation scores (see below) stabilized around 25-50 random steps (Figures S2. 3 & S2. 4). I therefore matched each observed step with 50 random steps with a turn angle and step length drawn from a Von Mises and Gamma distribution, respectively. All step lengths and turning angles (observed and random) were then log- and cosine-transformed respectively for analysis to obtain statistical coefficients that directly modify the movement distribution parameters fitted to observed steps (the Gamma shape and the Von Mises concentration parameters for step length and turning angle respectively; Duchesne et al. 2015; Avgar et al. 2016).

All possible combinations of predictors were then computed and models ranked according to Akaike Information Criterion (AIC) values, where the best supported model(s) were considered to be those within 2Δ AIC of the top model (Burnham & Anderson 2004).

Candidate models were excluded from this set if there were simpler nested versions with lower AIC values (Arnold 2010). Model fit was assessed using *k*-fold cross-validation adapted for conditional logistic regression, on 80% of randomly selected strata (groupings comprised of one observed and 50 random steps) to generate predictions for observed and random steps within the withheld strata 100 times (Fortin et al. 2009). This approach yields an average Spearman rank correlation (r_s) and associated 95% confidence intervals for observed (r_{obs}) and random steps (r_{rand}). Robust models are considered to have high r_{obs} relative to r_{rand}. Finally, to predict the effect of environmental and temporal covariates on juvenile movement from the fitted models (see Fig. 3. 3), I used the following equation:

$$Eq(1)\ Selection - free\ movement\ rate\ \left(\frac{metres}{40\ minutes}\right) = b_2 * [b_1 + \beta_{\log(step)} + (\beta_{(1\ldots n)} * x_{(1\ldots n)}]$$

where b_1 and b_2 are the tentative gamma shape and scale respectively, $\beta_{log(step)}$ is the estimated coefficient for the natural logarithm of step length 'log(step)', and $\beta_{(1\ldots n)}$ are the estimated coefficients for the interactions between covariates $x_{(1..n)}$ and 'log(step)' (Avgar et al. 2016; Ladle et al. 2019).

Unless otherwise indicated, all means in the Results are given ± standard deviation (SD).

3. 3 Results

3. 3. 1 General description of post-fledging movements

Juveniles fledged from Bird Island in May-June 2018 and 2019, and dispersed away from their natal colony at very large spatial scales, with two individuals conducting near-complete global circumnavigations within 5-7 months of fledging (Figures 3. 1a&b and Table 3. 1). Initially, all individuals fledged in a northeast direction towards South Africa, travelling on average 4435 ± 1471 km away from Bird Island within their first month at sea. Thereafter, movements were more restricted as most individuals remained within the southeast Atlantic and southwest Indian Oceans between 10°W-81°E and 50°-27°S (4006 ± 1776 km from Bird

Island). However, three juveniles travelled much further east reaching New Zealand, the southeast Pacific Ocean or southern Chile. One individual showed a third strategy, returning west towards South Georgia in its third month at sea and remaining within 1428 ± 583 km of the islands until the PTT stopped transmitting (see Figure S2. 1 for monthly distributions).

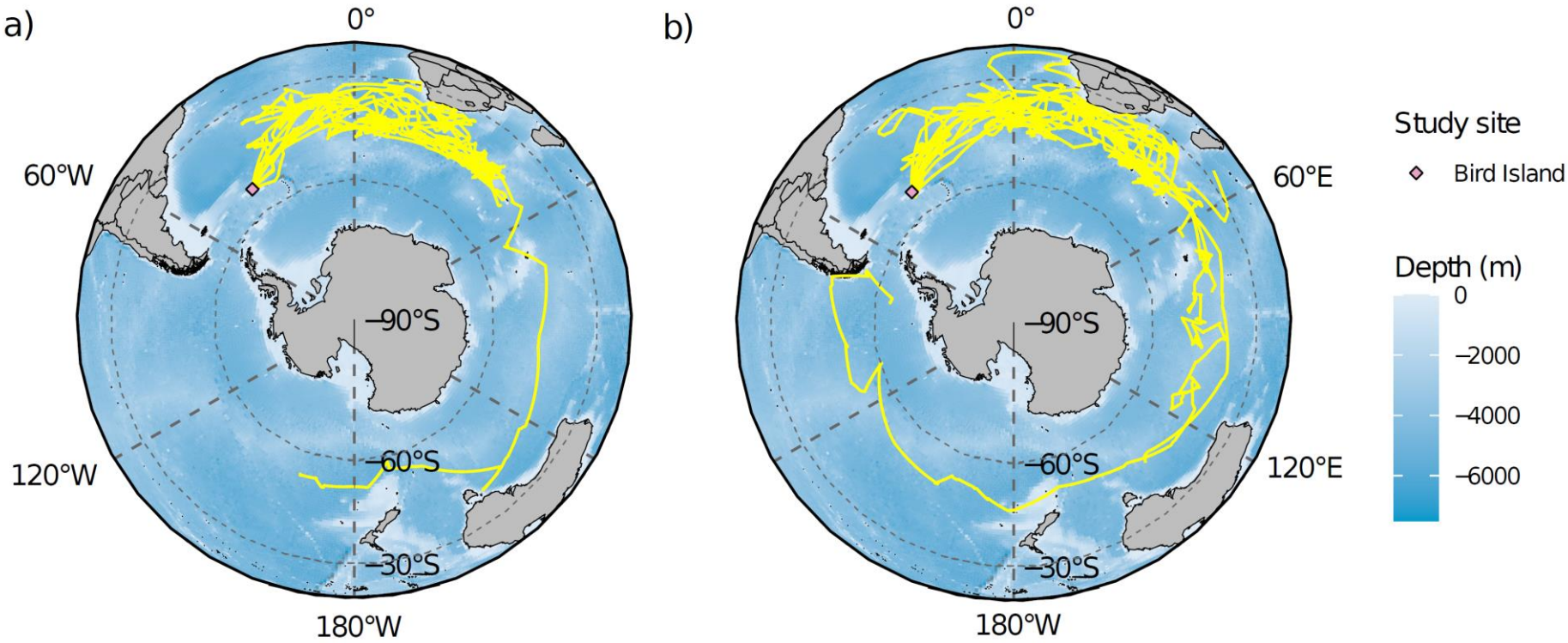

Figure 3. 1: At-sea distribution of juvenile grey-headed albatrosses tracked from Bird Island (South Georgia) in a) 2018 (n=9) and b) 2019 (n=14) using platform terminal transmitters (PTTs), and underlying bathymetry.

Table 3. 1: Summary of post-fledging movements of juvenile grey-headed albatrosses tracked from Bird Island (South Georgia) in 2018 and 2019 using Platform Terminal Transmitters (PTTs).

Month since fledging	Sample size	Calendar month(s)	Maximum distance from Bird Island (km; mean ± standard deviation)	Range	Oceanic regions used
1	23	May-July	4435 ± 1471	48.48W – 64.45E 56.04 – 18.48S	Southeast Atlantic & southwest Indian Oceans
2	20	June-August	5093 ± 1271	10.01W – 62.42E 49.56 – 15.69S	Southeast Atlantic & southwest Indian Oceans
3	16	July-August	5073 ± 1265	35.32W – 96.96E 53.29 – 31.31S	Central south Atlantic, southeast Atlantic, southwest Indian and central south Indian Oceans
4	12	August -September	6089 ± 1979	34.29W – 136.55E 51.66 – 37.49S	Central south Atlantic, southeast Atlantic, southeast and southwest Indian Oceans
5	6	September-October	5836 ± 2520	179.57W – 164.93E 60.50 – 39.43S	southwest Atlantic, southeast Atlantic, southwest Indian, and south Pacific Oceans
6	4	October-November	6427 ± 2928	80.92W – 142.79E 63.91 – 40.43S	Southeast Pacific, southeast Atlantic, southeast and southwest Indian Oceans
7	1	December	9370	169.74W – 179.26E 58.70 – 41.87S	southwest Pacific Ocean

3. 3. 2 Change in movement patterns and response to environmental conditions

Although there was some individual variation in monthly distributions, the best-supported *i*SSA provided strong evidence for a progressive change in behavior over time, indicated by the three-way interactions between month, wind speed and step length or turning angle in the two best-supported models (Table 3. 2). These models predicted that individuals moved faster and in a more directed manner, on average, during their first month at sea than during later months (positive coefficients for step length and turning angle in month 1; Figure 3. 2), and that higher wind speeds resulted in longer steps (~25 $km.hr^{-1}$ predicted increase in travel speed from wind speeds of 0 to 20 $m.s^{-1}$), and lower turning angles (Figures 3. 2, 3. 3b). Once in the southeast Atlantic (month 1; Figure 3. 3a), juveniles showed a significant and abrupt decrease in average travel speeds (of around 10-20 $km.hr^{-1}$, indicated by a drop in the step length coefficient in months 2-4 relative to month 1; Figures 3. 2, 3. 3b), and a progressive increase in path sinuosity over time (indicated by lower turning angle coefficient and hence, directional persistence, in months 2-4 relative to month 1; Figure 3. 2). During months 3 and 4, individuals appeared to settle in oceanic frontal regions (between the Subtropical and Polar fronts) (Figure 3. 3a), and responses to wind speed were minimal relative to month 1 (Figure 3. 2), even though individuals encountered similar conditions throughout the study duration (~ 0-20 and 0-17 $m.s^{-1}$ in months 1-2 and 3-4, respectively; Figure 3. 3b).

Table 3. 2: Predictors retained in best-supported conditional logistic regression models investigating the effects of winds ('wind'), chlorophyll a concentration (a proxy for prey resources; 'chl') and time (months since fledging; 'month') on the movement characteristics (step lengths; 'step', and turning angles; 'turn') of juvenile grey-headed albatrosses tracked from Bird Island (South Georgia) in 2018 (n=9) and 2019 (n=14) using Platform Terminal Transmitters (PTTs). Models including all possible combinations of the predictor variables were considered and ranked according to Akaike information criterion (AIC). Those reported below were within 2Δ of the best model. 'x' indicates predictor variables that were retained in top models; 'weight' the relative probability that a given model is the best model; R_{obs} and R_{rand} means and 95 confidence intervals are metrics of model performance generated using *k*-fold cross-validation adapted for conditional logistic regression

	Predictors																	
Model #	**step**	**step:month**	**step:chl**	**step:chl:month**	**step:wind**	**step:wind:month**	**turn**	**turn:month**	**turn:chl**	**turn:chil:month**	**turn:wind**	**turn:wind:month**	**df**	**AIC**	**ΔAIC**	**weight**	**R_{obs}**	**R_{rand}**
1	x	x	x	x	x	x	x	x	x	x	x	x	24	19358	0.00	0.69	0.554 ± 0.648	-0.006 ± 0.132
2	x	x	x	x	x	x	x	x	x		x	x	21	19359	1.58	0.31	0.560 ± 0.670	0.001 ± 0.151

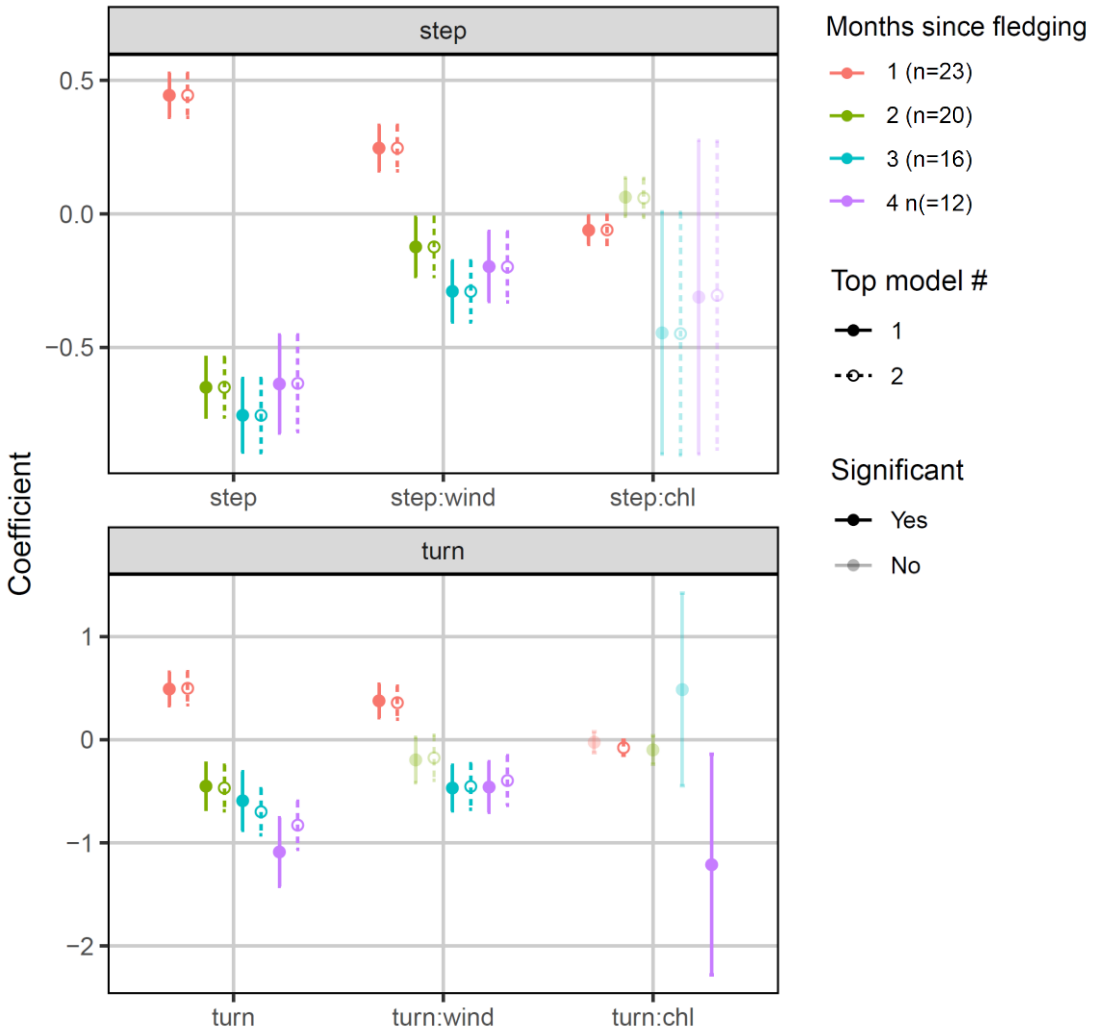

Figure 3. 2: Predicted effects of environmental conditions (winds 'wind' and chlorophyll a concentration as a proxy for prey resources 'chl') and time (months since fledging 'month') on the movement characteristics (step lengths 'step' and turning angle 'turn') of juvenile grey-headed albatrosses tracked from Bird Island (South Georgia) in 2018 (n=9) and 2019 (n = 14) using integrated step-selection analysis fitted using conditional logistic regression. Mean coefficients (dots) and 95% confidence intervals (error bars) were extracted from the best-supported models (Top models #1 and 2) ranked using Akaike information criterion (AIC), and represent average population effects for month 1 since fledging and change in average population effects relative to month 1 for months

2, 3 and 4 since fledging. A higher coefficient value for 'step' indicates increased travel speeds, while a higher coefficient for 'turn' indicates increased directional persistence, and hence, lower turning angles. Coefficients for which 95% confidence intervals contained 0 are considered to have a non-significant effect on juvenile movement characteristics and are displayed with reduced opacity.

Juveniles altered their movement characteristics in response to chlorophyll a, as both best-supported models retained three-way interactions between step length, chlorophyll a concentration and time, and one of the two models retained the three-way interaction between turning angle, chlorophyll a concentration and time (Table 3. 2). Juveniles decreased travel speeds in response to increasing productivity in month 1 as indicated by a negative interaction coefficient between step length and chlorophyll concentration, and to an increasing degree in months 3 and 4 (Figure 3. 2). As confidence intervals included zero however there appeared to be no significant effect over time (Figure 3. 2). As for turning angles, there was no consistent interaction between this movement characteristic and chlorophyll a concentration over time. The second most-supported *i*SSA model indicated that juveniles increased turning angles in areas of higher productivity regardless of month (slight negative interaction between turning angle and chlorophyll a concentration; Table 3. 2 and Figure 3. 2), while the most-supported model suggested this trend only occurred in the four month post-fledging when all juveniles reached frontal regions (Table 3. 2 and Figures 3. 2 & 3. 3a).

Finally, R_{obs} was relatively high compared to R_{rand} for both models suggesting results were robust (Table 3. 2).

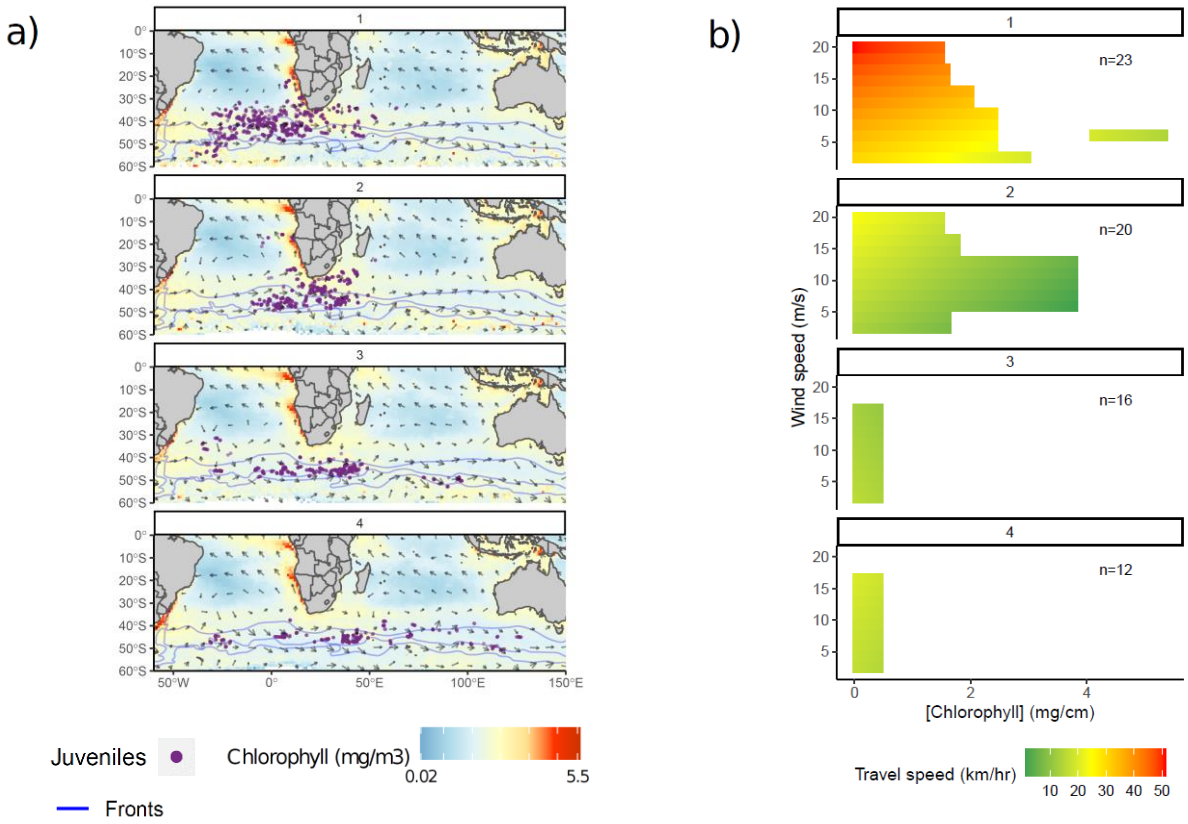

Figure 3. 3: a) Locations of juvenile grey-headed albatrosses tracked from Bird Island (South Georgia) in 2018 (n=9) and 2019 (n=14) using Platform Terminal Transmitters during their first four months at-sea [1, 2, 3, 4] in relation to chlorophyll a concentration, winds (speed and direction are represented by the direction and length of arrows, respectively) and three oceanic fronts (the Subtropical, Subantarctic and Antarctic Polar fronts from top to bottom; Orsi et al. 1995). The location of major fronts are shown in dark blue. b) Predicted change in juvenile travel speeds as a function of environmental (wind speed and chlorophyll concentration) and temporal covariates (months since fledging [1, 2, 3, 4]) using integrated step-selection analysis.

3. 4 Discussion

Using integrated step selection analysis (*i*SSA), I show a clear development in movement characteristics and responses to environmental conditions of juvenile albatrosses over the first four months post-fledging. Juveniles used winds to support fast and directed travel during their first month at sea and reduced their travel speeds when they encountered productive regions; thereafter, birds switched to progressively slower and more sinuous movements. These results provide new insights into the environmental cues driving behavioral decisions in naïve individuals, as well as the timing and development of broad-scale movement strategies in a very wide-ranging and long-lived seabird species.

3. 4. 1 Response to winds in dispersing juveniles

The ability to use prevailing winds efficiently to reach distant foraging grounds, thereby lowering travel costs, is well-established in oceanic seabirds, as well as in terrestrial birds, and is comparable to the use of ocean currents by swimming animals during long-distance migrations (Lambardi et al. 2008; Kemp et al. 2010; Afán et al. 2021). Adult seabirds often orient favorably with respect to wind direction, and by using crosswinds or tailwinds, they benefit from increased ground speeds or reduced energy expenditure associated with flapping (Weimerskirch et al. 2000b; González-Solís et al. 2009; Amelineau et al. 2014). Previous work has shown that juveniles of several seabird species are able to orient with respect to wind direction almost immediately after fledging, or learn to do so over the first few months at sea (Riotte-Lambert & Weimerskirch 2013; Collet et al. 2020; Syposz et al. 2021). In my study, fledglings were able to make use of prevailing westerlies to rapidly reach the productive frontal zones in the southeast Atlantic within their first month at sea, as they moved faster and in a more directed manner in response to increasing wind speeds. Thereafter, responses to winds were minimal, and speeds and directional travel were much reduced, suggesting juveniles had reached favorable foraging destinations, a pattern that was

broadly common to all the tracked individuals. This abrupt change in movement strategy lends increased support to the hypothesis that they use an innate compass (e. g. Perdeck 1958), whereby in this case, genetically coded information may guide these naïve individuals across a comparatively unproductive oceanic region, where locating patchy resources requires complex foraging abilities (Fauchald 1999), towards the extensive frontal region in the southeast Atlantic where prey is both predictable and plentiful. Indeed, this is an oceanographic area of high eddy activity as a result of the southerly Algulhas Return Current and the Antarctic Circumpolar Current interacting with bathymetry features, and is an important foraging area for several populations of adult grey-headed albatrosses; non-breeding and breeding individuals from South Georgia and Prince Edwards Islands, respectively (Nel et al. 2001; Clay et al. 2016).

Although juveniles responded less to variation in wind speeds after reaching waters southwest and south of Africa, it is likely that wind still plays a pivotal role in behavioral decisions given its importance for dynamic soaring flight, the dominant flight mode in albatrosses (Richardson 2011). Instead, the reduced dependence on winds at the large scale could reflect the improved ability of juveniles to make informed decisions of when and where, resulting in an intermittent use of winds to sustain shorter flight bouts in optimal foraging regions, similar to non-breeding adults (Mackley et al. 2010). It is however likely that juveniles require a long period of behavioural refinement in order to make optimal use of winds, as studies of other birds show that young can take months to years to reach travel speeds typical of adults (wandering albatross *Diomedea exulans*; Riotte-Lambert & Weimerskirch 2013), comparable soaring capability (white stork *Ciconia ciconia*; Rotics et al. 2016), or ability to compensate for wind drift (osprey *Pandion haliaetus* and honey buzzard *Pernis apivorus*; Thorup et al. 2003). Concurrent fine-scale tracking of both adults

and juveniles may provide further insights into the development of these skills in grey-headed albatrosses.

3. 4. 2 Response to resources: evidence for innate foraging abilities and progressive development of search strategies

Contrary to my expectations, juveniles responded to resource availability immediately after fledging by reducing their displacement rates and, to a lesser extent, their degree of directional persistence (trend only supported by the second best *i*SSA model). There was limited evidence for a progression in this response over time (a significant change in the interaction between turning angle and chlorophyll a concentration only in month 4). A similarly rapid adjustment of foraging behaviour in response to oceanographic proxies for prey availability (bathymetry and chlorophyll a concentration) has been shown for juvenile wandering albatrosses from the Crozet Islands (southern Indian Ocean; de Grissac et al. 2017). As acquiring resources is vital to survival, it could be that naïve individuals have an innate ability to interpret certain cues indicating good foraging conditions such as odor or water color (Nevitt 2000), or respond to the presence of foraging conspecifics (Thiebault et al. 2014).

My analysis also provided support for a significant change in broad-scale movement strategies over time, whereby juveniles reduced travel speeds and increased sinuosity after their first month at sea. This behavior, identified in young mollymawks and white-chinned petrels (*Procellaria aequinoctialis*) from the Indian Ocean (de Grissac et al. 2016), has also been demonstrated in adults when searching for food (e.g. Fauchald & Tveraa 2003; Weimerskirch et al. 2007; Louzao et al. 2011), and could indicate an improvement in the skills needed to locate prey over large spatial scales, such as flying across the wind to optimize the probability of encountering odor plumes (Nevitt et al. 2008), or to identify suitable prey whilst in flight, minimizing the high energy costs associated with unnecessary

landings and take-offs (Weimerskirch et al. 2000b; Clay et al. 2020). Alternatively, this behavior may have been triggered by the arrival of juveniles at frontal regions in months 3-4 post-fledging, where area-restricted search may be required to locate prey patches and swarms at finer scales in this type of habitat (Weimerskirch 2007). Regardless of the process underlying this behavioral transition, the development of large-scale search abilities may allow juveniles more generally to explore their surroundings, and sample a range of different oceanic conditions before adopting optimal migratory or foraging strategies in terms of preferred habitats or travel routes for instance (early-exploration-later-canalization hypothesis; Guilford et al. 2011; Votier et al. 2017; Collet et al. 2020).

3. 4. 3 Modelling environment drivers of movement: limitations and future opportunities

Modelling the environmental conditions experienced by individuals can be challenging given the variable temporal and spatial scales at which remotely-sensed variables are measured (Martin 2004). While the spatial resolution of wind speed and chlorophyll a data used in this study were considered to provide a good representation of the local environment (0.25°), modelling foraging conditions using a single proxy for prey availability is complicated given lags between biophysical processes (e. g. peak in primary production) and their effects at higher trophic levels (e. g. peak in seabird prey availability; Passuni et al. 2016). Here, I was able to detect the response of juveniles to monthly-averaged chlorophyll a concentrations; however, developing a global model of productivity which incorporates spatial and temporal dynamics in chlorophyll a variance might provide new insights into the main factors determining the timing of arrival and departure of individuals from specific foraging sites (e. g. Suryan et al. 2012). Indeed, juveniles in this study left the productive frontal region in the southeast Atlantic after their second month at sea and it is unclear whether this decision was

motivated by a seasonal depletion in resources (Koné et al. 2005) or other factors, such as increased intra- and inter-specific competition for prey (Abrams & Griffiths 1981).

Finally, *i*SSA provided a useful analytical framework for investigating the environmental mechanisms driving juvenile movements, and this modelling tool could easily be adapted to answer a wide range of questions. While I chose to focus on two simple environmental proxies for transport costs and productivity (or prey availability), a number of oceanographic parameters could be included in the model, thereby improving our understanding of the time needed for naïve individuals to learn how to interpret external cues of varying complexity (e.g. identification of mesoscale features such as ridges or seamounts which concentrate prey; Wakefield et al. 2009a). In addition, larger sample sizes and tracks of longer duration could facilitate investigation of whether individuals vary in their responses to the environment, and hence speed of learning, which may be a key trait determining the likelihood of successfully recruiting into the breeding population (Sergio 2014). Given that mortality is high in this age class, I highly recommend further research on the role of different cues in shaping movement patterns and the behaviors enhancing survival in early life, as these processes will be key to predicting and mitigating the impacts of climate change and other threats on the population trajectories of long-lived and wide-ranging marine species (Ong et al. 2015; Sherley et al. 2017; Rotics et al. 2017).

CHAPTER 4 – Tracking juveniles confirms fisheries-bycatch hotspot for an endangered albatross

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Author contributions:

I developed the research questions, conducted the data analysis and wrote up the chapter with supervision from R. A. Phillips & A. Manica.

C. Cunningham helped with obtaining funding for deploying the tracking devices described in this project, and provided feedback on all versions of the manuscript.

T. A. Clay performed a preliminary fisheries overlap analysis using tracking data from only 2018 (see section 4. 2. 2) and I used R code from this project to build the analysis used in this chapter. T. A. Clay also provided feedback on all versions of the manuscript.

S. Prince helped with obtaining funding for deploying the tracking devices described in this project, and provided feedback on all versions of the manuscript.

ABSTRACT

Fisheries bycatch is a major threat to marine megafauna such as seabirds. Population monitoring has revealed low survival of juvenile seabirds over recent decades, potentially because naïve individuals are more susceptible to bycatch than adults. However, major gaps remain in our knowledge of behavior and interaction of juveniles with fisheries. Here, juvenile grey-headed albatrosses (*Thalassarche chrysostoma*) were tracked from South Georgia - the largest global population of this endangered species, and in rapid decline - to investigate their at-sea distribution and assess bycatch risk. Fledged juveniles dispersed to the northeast, overlapping with a bycatch hotspot for grey-headed albatrosses reported by the Japanese pelagic longline fleet in the southeast Atlantic Ocean. Given adult grey-headed albatrosses use regions less exposed to fishing activity (< 40°S), the majority of birds bycaught in this area are probably juveniles from South Georgia, likely representing a key factor explaining the sustained population decline. This study highlights the urgent need to uncover the 'lost-years' for marine megafauna to enable focused conservation efforts.

4. 1 Introduction

Incidental mortality (bycatch) of seabirds in fisheries is a major conservation problem affecting numerous species worldwide, in particular albatrosses and large petrels (Phillips et al., 2016). These long-lived birds have extensive ranges which bring them into potential conflict with diverse fleets across the globe, and even small reductions in their survival have dramatic impacts on population dynamics (Arnold et al. 2006; Clay et al. 2019; Carneiro et al. 2020). Initial evidence of this threat came from recoveries of ringed birds in longline fisheries in the 1980s (Croxall & Prince 1990). Electronic tracking has since become an essential tool for identifying potential bycatch hotspots, as tracks can be overlaid on the distribution of fishing effort, helping to focus conservation efforts in time and space (Croxall & Nicol 2004; Suryan et al. 2007; Copello et al. 2014).

The year-round distribution and bycatch risk of adults is known for many species of albatrosses and large petrels; however, major gaps remain in our knowledge of distributions of juveniles and immatures (Carneiro et al. 2020). These younger life-history stages are challenging to track because of the long periods spent at sea between independence and first return to breeding colonies, termed the ‘lost years’ (Hazen et al. 2012). However, existing studies suggest that juveniles disperse more widely than migrating adults, potentially increasing exposure to bycatch risk (Weimerskirch et al. 2006; Trebilco et al. 2008; Afan et al. 2019; Chapter 2). As juveniles and immatures account for >50% of the population of certain species, high juvenile mortality can hamper the recovery of threatened seabirds, and even cause population decline if chronic mortality substantially reduces recruitment (Weimerskirch et al. 1997a; Pardo et al. 2017; Carneiro et al. 2020). Understanding age-related differences in movement patterns is therefore a priority for informing effective bycatch-mitigation strategies.

The grey-headed albatross (*Thalassarche chrysostoma*) was uplisted from Vulnerable to Endangered in 2018 by IUCN (IUCN, 2019), largely due to the continued steep decline of by far the largest global population, which breeds at South Georgia (Poncet et al. 2017). Their circumpolar distribution and propensity to forage at oceanic frontal zones brings them into potential conflict with fisheries, particularly pelagic longlines targeting tuna and billfishes (Scombridae) within multiple Regional Fisheries Management Organizations (RFMOs; Croxall, 2005; Clay et al., 2016, 2019). However, a recent assessment of bycatch risk of adult birds concluded that spatial overlap with fishing effort was lower than in other sympatric albatrosses, and likely insufficient to account for the steep population decline (Clay et al. 2019). Nonetheless, over the last few decades (between 1997 and 2015) observers on Japanese vessels have reported high bycatch of grey-headed albatrosses in the central southeast Atlantic Ocean (35-45°S, 10°W-20°E) (Inoue et al. 2012; Katsumata et al. 2017). The provenance of these birds has been a puzzle, as the region is rarely used by adults from either South Georgia or Indian Ocean colonies (Clay et al. 2016), thereby indicating that other life-history stages (such as juveniles) may be particularly susceptible.

Here, I examine overlap between pelagic longline fisheries operating in the South Atlantic, Indian and Pacific Oceans and grey-headed albatrosses from South Georgia, incorporating new tracking data collected in 2018 and 2019 from juveniles. I aimed to fill key gaps in knowledge of at-sea distribution of juveniles and compare their potential bycatch risk with adults, describing monthly variation in movement patterns and fisheries overlap, and identifying periods, regions and fleets of greatest concern.

4. 2 Methods

4. 2. 1 At-sea distribution of juveniles and adults

4. 2. 1. 1 Tracking data processing

Tracking data were obtained from adult and post-fledgling juveniles from Bird Island, South Georgia (54°00'S, 38°03'W). Duty-cycled Platform Terminal Transmitters (PTTs) were deployed on grey-headed albatross (GHA) chicks prior to fledging in May-June 2006, 2018 and 2019. Seven PTTs were deployed in 2006 (for details see Clay *et al.* [2019]), and 16 PTTs (Telonics TA-2630) in both 2018 and 2019. Seven and two chicks in 2018 and 2019, respectively, died before leaving the island, or shortly thereafter (probably depredated by giant petrel *Macronectes spp.*), as transmissions at sea ceased within 1 day. Between 24 and 940 locations were obtained from each of the remaining PTTs (n = 28), covering a period between May and December (see Table 4. 1 for complete metadata). Tracking data for breeding and non-breeding adults were collected between 1993 and 2012 using PTTs, GPS (Global Positioning System) loggers and geolocators (Global Location Sensors or GLS) (for deployment details, see for e. g. Phillips et al. 2004c; Clay et al. 2016). In all cases, the total mass of devices including attachments were less than the 3% threshold of body mass beyond which deleterious effects are more common in oceanic seabirds (Phillips et al. 2003).

All locations from PTTs in ARGOS classes A, B, 0, 1 and 3 were used, but unrealistic positions requiring a sustained flight speed of over 90 $km.h^{-1}$ were removed (McConnell et al. 1992). Light data from geolocators were processed using MultiTrace Geolocation or BASTrak software, providing two positions per day with a mean error of 186 ± 114 km (Phillips et al. 2004a). Locations with interruptions around sunrise and sunset, and periods for 3-4 weeks around the equinoxes when latitude cannot be estimated reliably, were excluded. PTT and GPS data were interpolated at hourly intervals to obtain regular positions. GLS data were not interpolated as locations are available at regular, approximately 12-hour, intervals. In total, 329 tracks from 156 adults were used in analyses (Incubation: 25 tracks from 25 individuals; Brood: 86 tracks from 63 individuals, Post-Brood: 158 tracks from 20 individuals and Non-breeding: 55 tracks from 55 individuals).

A resampling procedure was carried out to determine whether sample sizes for juveniles were sufficient to represent population-level space use, as in Clay *et al.* (2019). This was not the case, and therefore although 28 juveniles were tracked, the subsequent analysis represents the at-sea distribution of the sampled individuals and may underestimate the actual population distribution (Appendix S3. 1). I therefore conducted a sensitivity analysis to assess the effect of sample size on relative overlap with pelagic longline fisheries (described below in 2.2.2). As for adults, a previous gap analysis indicated that sample sizes were adequate to represent home ranges during all breeding and nonbreeding periods (Clay et al. 2019).

4. 2. 1. 2 Generating juvenile and adult at-sea distributions

Monthly distribution grids for juveniles and adults were generated using kernel analysis in the *adehabitatHR* package (Calenge 2006). A fixed smoothing parameter (h) of 50km or 200km was used for PTT and GPS data, and for GLS data, respectively, and a grid cell size of 10km was used for all device types to enable averaging across grids. Interpolated hourly PTT and GPS data from the same breeding stage were pooled before kernel analysis. If PTT and geolocator data were available for the same breeding stage, distribution grids were weighted according to sample size before merging the two datasets. Grids were generated for all months if sample sizes for each life-history stage were ≥ five individuals (May – September). A rectangle corresponding to the bycatch hotspot reported in the southeast Atlantic Ocean (International Commission for the Conservation of the Atlantic Tunas [ICCAT] subareas 6, 7 and 8 during quarters 2 and 3; Inoue et al. 2012; Katsumata et al. 2017) was overlaid on these grids and maps of spatial overlap with fishing effort (see below).

4. 2. 2 Analysis of spatial overlap between GHA and fisheries

4. 2. 2. 1 Fishing effort data

Effort data for pelagic longline fisheries (number of hooks deployed, by 5 x 5° square) were collated for all tuna RFMO from publicly available databases: Indian Ocean Tuna

Commission (IOTC), ICCAT, Western and Central Pacific Fisheries Commission (WCPFC), Inter-American Tropical Tuna Commission (IATTC). Effort data from the Commission for the Conservation of Southern Bluefin Tuna (CCSBT) were not considered as these data are also reported to the other four RFMOs (Clay et al. 2019). Monthly effort data were available for all RFMOs except WCPFC, for which quarterly effort data was converted into monthly estimates by dividing effort equally. Although effort may not have been consistent over time, this assumption is unlikely to have affected results as WCPFC contributed little to overlap scores (see Tables S3. 2 and S3. 3). Where the areas of competence of RFMOs overlapped in space (i.e. double-reporting), duplicate values were filtered by choosing the maximum number of hooks reported by a given fleet to the RFMOs for a given 5 x 5° grid square. Analyses were of the monthly mean effort for the period 2010-2018.

4. 2. 2. 2 Risk analysis

Monthly spatial overlap between tracked juveniles and adults, and pelagic longline fishing effort was calculated by multiplying the number of hooks by the proportion of the distribution of each life-history stage in each 5 x 5° square, by month (similarly to Clay et al. 2019; Carneiro et al. 2020). I used a jackknife procedure (i.e., withholding one individual bird in turn) to determine the sensitivity of the monthly overlap scores to the sample of tracked birds.

All data manipulations and analyses were conducted in R ver. 3.6.2. (R Core Team 2020).

4. 3 Results

4. 3. 1 At-sea distribution of juvenile and adult GHA

Table 4. 1: Deployment metadata for juvenile grey-headed albatrosses tracked from Bird Island, South Georgia, in 2006, 2018 and 2019 using Platform Terminal Transmitters (PTTs).

Year	Device type	Duty-cycling regime	No. PTTs deployed	Tracks retained post-processing	No. locations per track	Mean ± SD track duration in days	Tracking period
2006	Microwave PTT-100	24h on, 48h off	7	5	24 – 53	17.2 ± 6.0	5 May – 6 June
2018	Telonics TAV-2630	8h on, 48h off	16	9	260 – 940	101.1 ± 47.5	24 May – 12 December
2019	Telonics TAV-2630	8h on, 48 off	16	14	53 – 849	82.7 ± 54.3	12 May – 27 October

Juvenile grey-headed albatrosses were tracked for 17-101 days after fledging in May-June from Bird Island (Figure 4. 1), with the last transmissions received by the ARGOS system in July, December and October in 2006, 2018 and 2019, respectively (see Table 4. 1 for full metadata). Initially, juveniles dispersed in a northeast direction from South Georgia, then moved towards the southeast Atlantic, overlapping with ICCAT subareas 6, 7 and 8 (predominantly in May-June, although overlap of a number of birds persisted until September; Figure 4. 2a). Thereafter, one juvenile moved northwards towards the Namibian and Angolan coastlines (July; Figure 4. 2a), and the remainder continued progressively eastwards to the southwest Indian Ocean (July; Figure 4. 2a). Three individuals dispersed even further east, reaching the southeast Indian Ocean (August; Figure 4. 2a), New Zealand (September; Figure 4. 2a), and southern Chile (October onwards - one individual only; Figure 4. 1). PTT transmissions ceased at different points in time, so it remains unclear whether

more juveniles would have dispersed as far (Table 4. 1). Adult grey-headed albatrosses also made considerable use of the southwest Indian Ocean in the nonbreeding season (June – September; Figure 4. 2b). However, in contrast to juveniles, adults were more broadly distributed during May – September (Figure 4. 2b), using the southwest Atlantic (May – September; Figure 4. 2b), southeast Pacific (May; Figure 4. 2b) and southwest Pacific (September, Figure 4. 2b) Oceans. When in the southeast Atlantic Ocean, adults remained largely south of 45°S, and therefore unlike juveniles, only a tiny proportion of their distribution (< 0.005% vs. [0.05-0.1%] per month for adults and juveniles respectively) overlapped with ICCAT subareas 6, 7 and 8 in May–June (Figure 4. 2a & b).

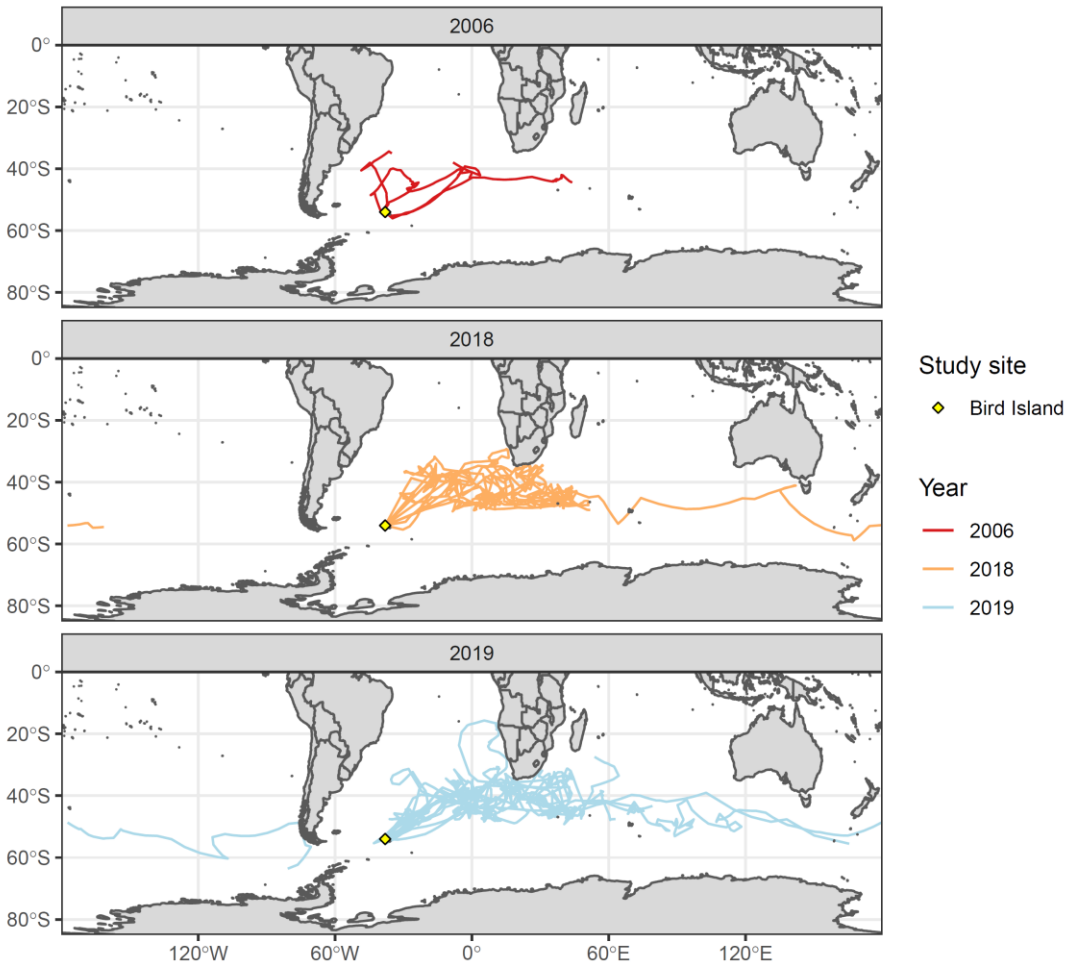

Figure 4. 1: At-sea distribution of juvenile grey-headed albatrosses tracked from Bird Island, South Georgia, in 2006 (n=5), 2018 (n=9) and 2019 (n=14).

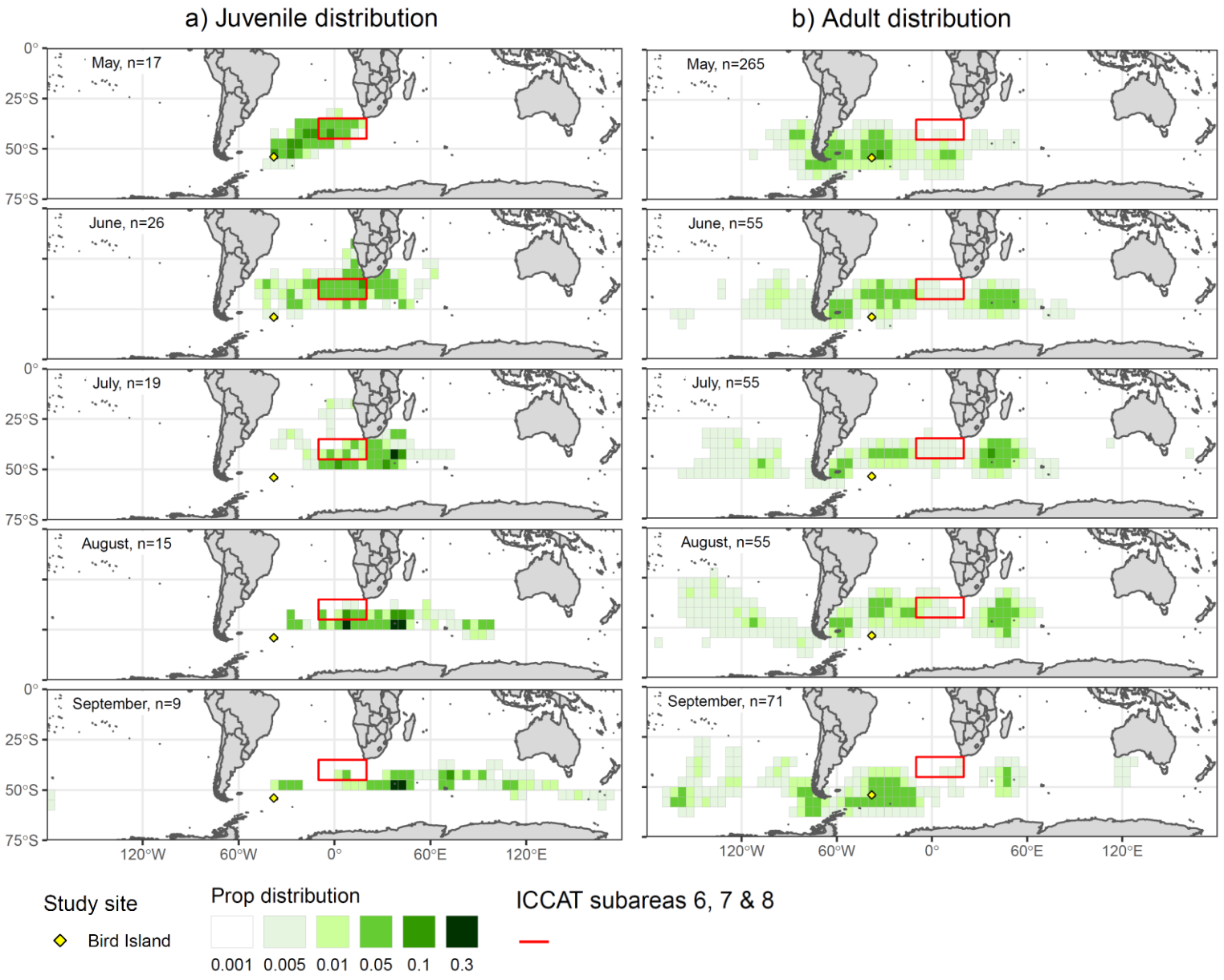

Figure 4. 2: Monthly (May-September) distribution in 5x5° cells of a) juvenile and b) adult grey-headed albatrosses tracked from Bird Island, South Georgia. 'Prop distribution' represents the proportion of the monthly distribution occurring in each 5x5° square. A bycatch hotspot for grey-headed albatrosses was reported in ICCAT subareas 6, 7 and 8 for April-June, 1997 – 2015 (Inoue et al. 2012; Katsumata et al. 2017), and for July-September 1997-2009 (Inoue et al. 2012)

4. 3. 2 Fisheries bycatch overlap risk of juvenile and adult GHA

Average annual pelagic fishing effort in 2010-2018 was high in various regions intensively used by juveniles and adults; in particular within ICCAT subareas 6, 7 and 8 (5 x 5° grid cells with up to 2 million hooks deployed annually; Figure 4. 3a) as well as the southwest Indian Ocean (5 x 5° grid cells with up to 20 million hooks annually; Figure 4. 3a). As a result, overlap scores, and hence bycatch risk, were correspondingly high in the former region for juveniles, and the latter region for both life-history stages (Figure 4. 4a & b). Overlap with pelagic longline effort was highest for juveniles in May – July (85 – 143 [jackknife range: 66 – 149] x 10^3 hooks; Figure 4. 5a) in accordance with annual peaks in monthly pelagic longline effort in ICCAT subareas 6, 7 and 8 (up to 2.1 million hooks in May; Figure 4. 3b), and dominated by the Japanese, South Korean and Taiwanese fleets in the southeast Atlantic in May – June (Figures 4. 4a & 4. 5a), and by the Taiwanese fleet in the southwest Indian Ocean in June – July (Figures 4. 4a & 4. 5a). Juveniles also overlapped to some extent with the Malaysian, Namibian, Seychellois, and Spanish fleets (Figure 4. 5a). Adults also overlapped with the Taiwanese fleet in the southwest Indian Ocean, predominately in June – August (Figures 4. 4b & 4. 5b), and to a lesser extent with the Japanese, South Korea and Taiwanese fleets in the southeast Atlantic (mainly in June; Figures 4. 4b & 4. 5b), and with the Chinese, Taiwanese and Vanuatuan fleets in the southwest Pacific Ocean (mainly in August; Figures 4. 4b & 4. 5b). However, overlap scores with pelagic longline effort of

tracked adults were much lower than those of juveniles (21 – 22 [jackknife range: 17 – 22] hooks x 10^3 in June – August; Figure 4. 5b). Jackknifing of overlap scores revealed that bycatch risk was consistently higher for juveniles than adults in months of highest overlap (May – June; Figure S3. 2). Thus, although the sample size for juveniles was lower (Figure 4. 2), overlap scores were robust to the selection of individuals within the tracked sample.

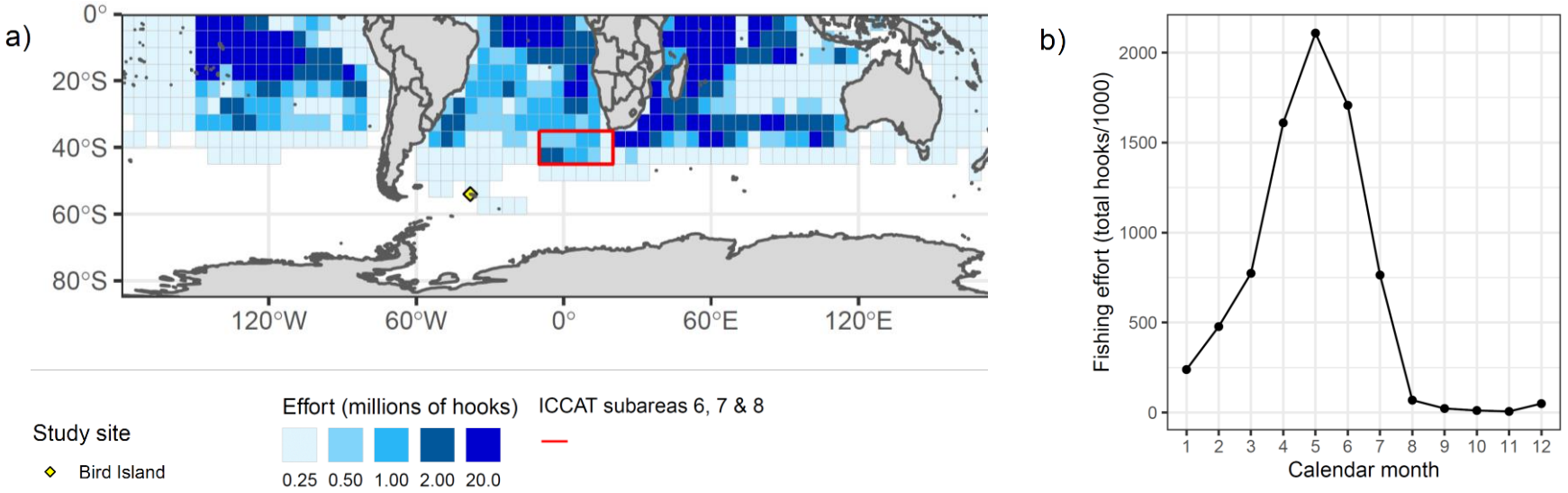

Figure 4. 3: a) Mean annual distribution of pelagic longline effort over the period 2010-2018. A bycatch hotspot for grey-headed albatrosses was reported in ICCAT subareas 6, 7 and 8 for April-June, 1997 – 2015 (Inoue et al. 2012; Katsumata et al. 2017), and for July-September 1997-2009 (Inoue et al. 2012) b) Mean monthly variation in pelagic longline effort over the period 2010-2018 for ICCAT subareas 6, 7 and 8.

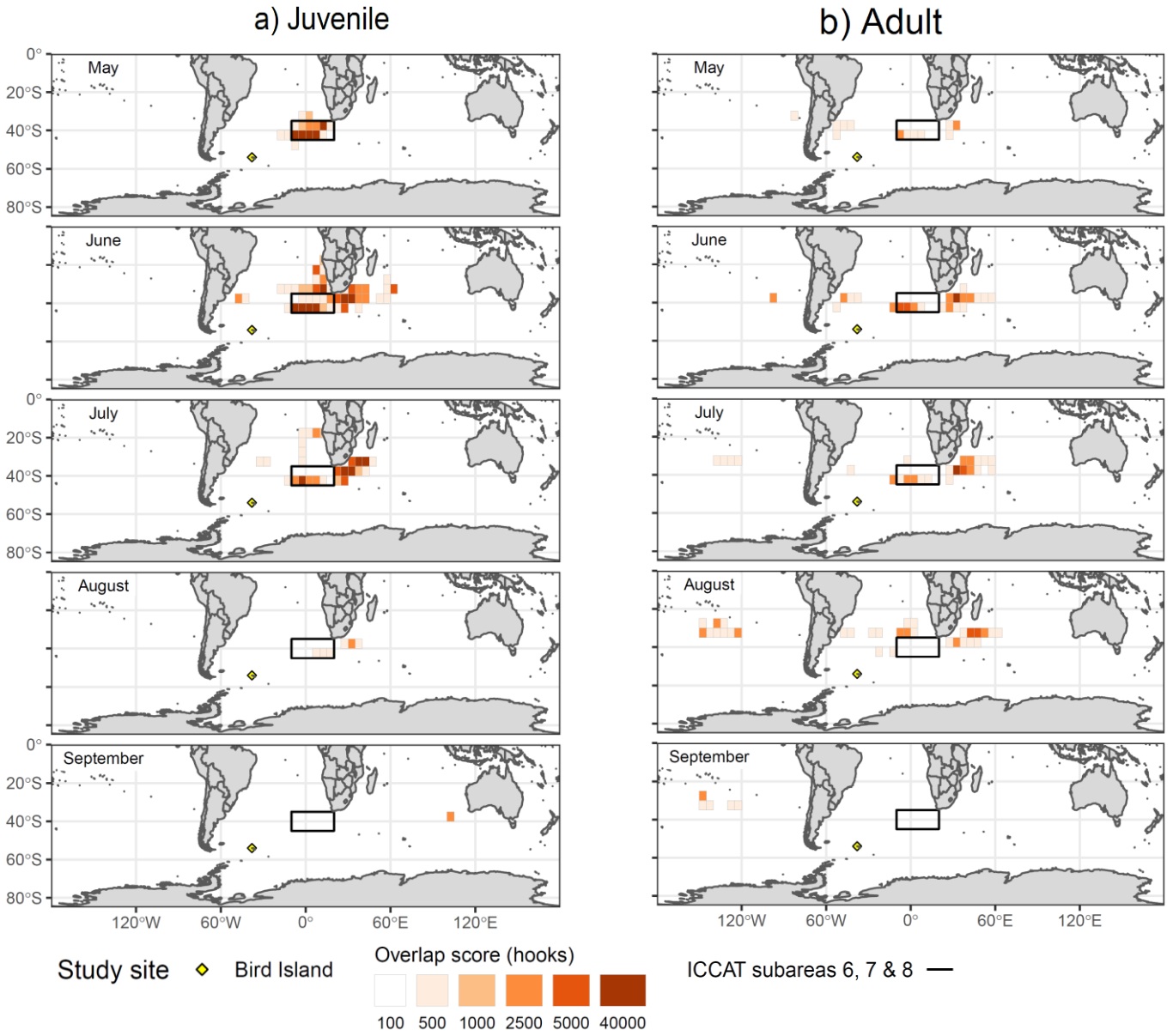

Figure 4. 4: Monthly overlap score of a) juvenile and b) adult grey-headed albatrosses tracked from Bird Island, South Georgia, at-sea distribution with pelagic longline fishing effort averaged over the 2010-2018 period. A bycatch hotspot for grey-headed albatrosses was reported in ICCAT subareas 6, 7 and 8 for April-June, 1997 – 2015 (Inoue et al. 2012; Katsumata et al. 2017), and for July-September 1997-2009 (Inoue et al. 2012).

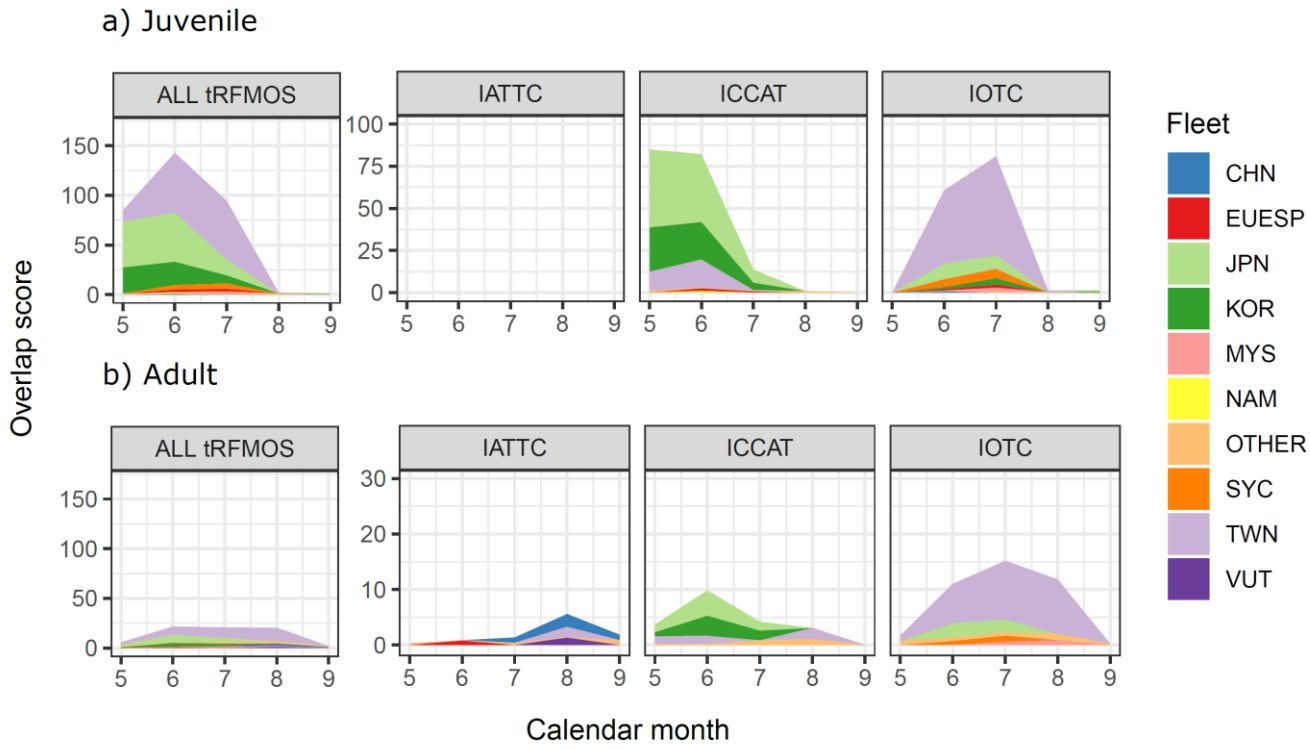

Figure 4. 5: Stacked overlap scores (hooks.10^3; see Tables S3. 2 & 3. 3 for exact values) of a) juvenile and b) adult grey-headed albatrosses tracked from Bird Island, South Georgia, with pelagic longline fishing effort by tuna regional fisheries management organization (tRFMOS; IATTC = Inter-American Tropical Tuna Commission, ICCAT = International Commission for the Conservation of Atlantic Tunas, IOTC = Indian Ocean Tuna Commission) and fleet (CHN = China, EUESP = Spain, JPN = Japan, KOR = South Korea, MYS = Malaysia, NAM = Namibia, SYC = Seychelles, TWN = Taiwan, VUT = Vanuatu). Overlap with fleets from the Western and Central Pacific Fisheries Commission (WCPFC) was minimal and not included in this figure (Tables S3. 2 & S3. 3). Note that the scale of the y-axis differs for juveniles and adults.

4. 4 Discussion

By comparing the at-sea distributions of juveniles and adults, I show that a reported bycatch hotspot for grey-headed albatrosses in the southeast Atlantic corresponds to a previously unknown staging area used by juveniles fledging from the largest global population of this

endangered species. These results highlight the importance of understanding within-population variation in movement patterns and are discussed in the context of focusing efforts on fisheries-bycatch mitigation.

4. 4. 1 Life-history stage and at-sea distributions

The most striking difference in the at-sea distributions of adults and juveniles was in May – June, corresponding to the period of dispersal at the end of breeding. During this time, juveniles travelled rapidly northeast from the natal colony, while adults made use of more southerly regions around South Georgia, the southwest Indian and Pacific Oceans. While the tracking data does not represent the movements of all individuals, juveniles used this narrow dispersal corridor in all three study years, suggesting that this route is important for the majority of birds from this population. Directed initial flight is common to juveniles of other albatross and petrel species (Weimerskirch et al. 2006; Gutowsky et al. 2014; de Grissac et al. 2016), and suggests their initial path is guided by an innate compass (Åkesson & Weimerskirch 2005; de Grissac et al. 2016), which may help individuals reach distant foraging areas and reduce competition for resources between age classes (Gutowsky et al. 2014; Chapter 2). After these first few months, juveniles continued east, mirroring two of the three migration strategies used by non-breeding adults: movement to wintering sites in the southwest Indian Ocean and circumpolar migrations (Croxall et al. 2005). Longitudinal tracking of birds over multiple years may show some juveniles eventually adopting the third strategy of nonbreeding adults - remaining within the breeding range - as it seems likely that individual exploration during the first year post-fledging determines foraging specializations used by adults throughout their lifetime (Campioni et al. 2020).

4. 4. 2 Implications for overlap with pelagic longline fishing effort

As a result of their divergent movement patterns, adults and juveniles varied in the extent to which they overlapped with pelagic longline effort. In areas with high fishing intensity, birds

are more likely to encounter and be caught by fishing vessels, hence it can be assumed that juveniles have a higher mortality risk than adults, which may be compounded by their naïve foraging behavior (Gianuca et al. 2017). In particular, juveniles may scavenge disproportionately behind vessels because of lower foraging efficiency or be less able to avoid fishing gear (Jiménez et al., 2016). Soon after fledging (May – June), the tracked juveniles in this study reached the southern limit of high-intensity fishing effort in the southeast Atlantic, including the reported bycatch hotspot for this species in ICCAT subareas 6, 7 and 8. Although the age-class of bycaught birds in this region is unknown, tracked adults remained largely south of 45°S, and hence it is almost certain that a substantial proportion of the grey-headed albatrosses killed in this region are juveniles from South Georgia. There is also the possibility that some birds are from breeding sites in the Indian Ocean (Nel et al. 2001; Clay et al. 2016). However, given that juveniles in this study dispersed eastwards following prevailing winds, it may be that juveniles from other populations fledge in a similar direction and consequently use other oceanic regions in May – June (southwest Indian Ocean, Pacific Ocean…). In addition, the overlap analyses identified two other fleets of major concern: Taiwan and South Korea in the same region in May - June, and Taiwan in the southwest Indian Ocean in June – July. There are some reports of bycaught grey-headed albatrosses in these regions by both fleets, but observer coverage is variable and generally low (Taiwan: 3-10.4% and South Korea: 7-24%; Huang, 2017; Kim et al., 2019), and seabird mortality will therefore be greatly underestimated. From August-September onwards, a greater proportion of the tracked juveniles travelled southeast towards areas of lower pelagic longline fishing effort, and so bycatch risk probably reduced to levels in line with those of the tracked adults (Fig. 4. 2b). Finally, the sensitivity analysis indicated that overlap scores varied little according to the subset of tracked individuals that were included in the analysis, suggesting that sample sizes were adequate to robustly assess relative bycatch risk of

juveniles and adults from this population during the period of highest risk (May – September).

4. 4. 3 Conclusions and recommendations

Here I identify high overlap between the distribution of juvenile grey-headed albatrosses during the first months post-fledging and three major pelagic longline fleets: Japan, South Korea and Taiwan. My results therefore confirm that a major bycatch hotpot reported by Japanese fisheries observers in the southeast Atlantic Ocean (Inoue et al. 2012; Katsumata et al. 2017) is likely to be of juveniles from South Georgia. Given the continued decline of this globally-important population, reducing bycatch by these fleets would play a crucial role in reducing extinction risk, especially as poor juvenile survival will suppress recruitment rates and cause population decline (Pardo et al. 2017). I thus strongly recommend improved monitoring of bycatch rates, introduction of mandatory best-practice seabird-bycatch mitigation, and close compliance-monitoring either by independent observers or by using tamper-proof cameras on these vessels in the areas and periods of greatest overlap. I also encourage further tracking of under-studied life-history stages in other seabirds with high bycatch susceptibility.

CHAPTER 5 – Effects of age on foraging behaviour in two closely related albatross species

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Author contributions:

I conceived the project, developed the research questions, conducted the data analysis and wrote up the chapter with supervision from R. A. Phillips & A. Manica.

ABSTRACT

Background: Foraging performance is widely hypothesized to play a key role in shaping age-specific demographic rates in wild populations, yet the underlying behavioral changes are poorly understood. Seabirds are among the longest-lived vertebrates, and demonstrate extensive age-related variation in survival, breeding frequency and success. The breeding season is a particularly critical phase during the annual cycle, but it remains unclear whether differences in experience or physiological condition related to age interact with the changing degree of the central-place constraint in shaping foraging patterns in time and space.

Methods: Here I analyze tracking data collected over two decades from congeneric black-browed (BBA) and grey-headed (GHA) albatrosses, *Thalassarche melanophris* and *T. chrysostoma*, breeding at South Georgia. I compare the foraging trip parameters, at-sea activity (flights and landings) and habitat preferences of individuals aged 10-45 years and contrast these patterns between the incubation and early chick-rearing stages.

Results: Young breeders of both species showed improvements in foraging competency with age, reducing foraging trip duration until age 26. Thereafter, there were signs of foraging senescence; older adults took gradually longer trips, narrowed their habitat preference (foraging within a smaller range of sea surface temperatures) (GHA), made fewer landings and rested on the water for longer (BBA). Some age-specific effects were apparent for each species only in certain breeding stages, highlighting the complex interaction between intrinsic drivers in determining individual foraging strategies.

Conclusions: Using cross-sectional data, this study highlighted clear age-related patterns in foraging behavior at the population-level for two species of albatrosses. These trends are likely to have important consequences for the population dynamics of these threatened

seabirds, as young or old individuals may be more vulnerable to worsening environmental conditions.

5. 1 Introduction

Aging is ubiquitous in wild vertebrates, with important consequences for population dynamics, and the ecological and evolutionary processes promoting species diversity and co-existence (Bonsall 2006; Nussey et al. 2013; Jones et al. 2014). A range of fitness components vary with age (as reviewed in Nussey et al. 2013). These are predicted to explain why survival probability and reproductive success increase in early life, as individuals acquire skills and experience, and decline in old age due to senescence (Kirkwood & Rose 1991; Sydeman et al. 1991; Monaghan et al. 2008). In reality, the rates, onset, and trajectory of aging often depart from this pattern and vary greatly among and within species (Gaillard et al. 1989; Calder 1996; Bonduriansky et al. 2008). Moreover, the underlying mechanisms are poorly understood, and researching the proximate drivers has become a key topic in the study of aging with wide-ranging implications for life-history theory, population ecology, and wildlife management (Lemaitre et al. 2015; Markussen et al. 2018; Rocha El Bizri et al. 2019).

Foraging performance is likely to play an important role in shaping the aging process as extracting resources from the environment determines the amount of energy or nutrients animals can allocate to maintenance or reproduction, with consequences for current and future reproduction, and survival (Boggs 1992; Stearns 1992). Foraging ability is known to improve in early life, reflecting the development of physical abilities, or the gain in experience of locating and catching prey (Gasparini et al. 2002; Yoda et al. 2004; Gunst et al. 2010). Acquiring these skills can directly improve survival probability, and foraging performance can continue improving past sexual maturity as animals learn to adapt to the added constraints of breeding (Daunt et al. 2007b). Evidence for age-related variation in foraging behavior in later life is rarer, and more difficult to interpret. Differences between old and young adults in activity budgets, diets, distribution, habitat use and other foraging

characteristics have been linked to physiological declines (Catry et al. 2006; MacNulty et al. 2009; Montgomery et al. 2013), with consequences for fitness in some instances (Hassrick et al. 2013; Clay et al. 2018; Patrick & Weimerskirch 2015). However, changes in foraging behavior with age may not be detectable if individuals are able to compensate for physiological aging, warranting further investigation across multiple taxa (Elliott et al. 2014; Phillips et al. 2017).

Seabirds, and albatrosses in particular, are excellent models for studying aging as they are among the longest-lived vertebrates, with some individuals reaching over 60 years of age (Wasser & Sherman 2010; Weimerskirch 2018). Long-term monitoring studies demonstrate considerable age-related variation in their reproductive performance (Pardo et al. 2013; Patrick & Weimerskirch 2015; Froy et al. 2017), and remote-tracking techniques provide effective tools for investigating their foraging behavior (Jouventin & Weimerskirch 1990; Xavier et al. 2003; Clay et al. 2016). Albatrosses cover remarkable distances while foraging at sea, but their energetic requirements and reproductive demands change throughout the year, limiting foraging in time and space to different extents (Weimerskirch et al. 2014; Phillips et al. 2017). The breeding period is an especially critical phase during their annual cycle, as individuals are under strong selection to forage efficiently in order to relieve fasting partners during incubation, and to feed both themselves and their young during chick-rearing (Phillips et al. 2017). Inexperience may be a constraint in young breeders if they are less-skilled at acquiring prey items (Navarro et al. 2010; Le Vaillant et al. 2012; Haug et al. 2015). Reduced physiological condition in older breeders may have a similar effect, manifested as extended foraging trips, reduced foraging effort, or differential habitat use in the few seabird studies to date (Lecomte et al. 2010; Catry et al. 2011; Jaeger et al. 2014). As these findings largely relate to analyses from a single breeding stage, it remains unclear however *how* these intrinsic attributes interplay with the changing degree of the central-place

constraint in shaping foraging patterns in time and space. Investigating this question will provide crucial insight into the ecological forces shaping aging trends and driving the population dynamics of this highly threatened group of seabirds (Phillips et al. 2016).

Here I performed a cross-sectional study to investigate the links between age, foraging behavior and breeding stage in grey-headed and black-browed albatrosses, *Thalassarche chrysostoma* and *T. melanophris* (hereafter GHA and BBA, respectively) tracked from Bird Island, South Georgia, between 1997 and 2015. GHA and BBA are closely-related, similar in size and breeding cycle but differ in aspects of their life-history strategies (breeding frequency, lifespan and age-specific breeding success; Prince et al. 1994b; Burg & Croxall 2001; Phillips et al. 2004c; Froy et al. 2017). In particular, only in GHA are there signs of senescence in reproductive success (Froy et al. 2017). This accords with some evidence of longer trip durations and reduced foraging efficiency in older breeders during incubation (Catry et al. 2006). Here, I build on that initial tracking study by incorporating movement and activity data from multiple breeding stages and study years for both GHA and BBA, to investigate whether species-specific aging trajectories may be driven by differences in foraging behavior. Specifically, I hypothesize that young adults of both species may have reduced foraging competency, and therefore take longer trips to less-productive areas, and have a higher take-off and landing rate, as they may be less skilled at finding or handling prey. As only GHA show signs of reproductive senescence, I hypothesize that only this species will show signs of foraging senescence, by taking longer foraging trips, and spending a larger proportion of these trips resting on the water as a result of physical deterioration. For the same reasons, I expect old GHA to differ from younger birds in habitat use, targeting less productive or more accessible foraging areas (Wakefield et al. 2009b). Finally, I contrast these patterns between breeding stages, expecting age effects to be more pronounced during incubation when the central-place constraint is less severe and individuals conduct long-range

trips (Phillips et al. 2004c). I also expect age effects to differ between sexes, given the degree of sexual dimorphism in wing loading and wing area, and evidence for spatial segregation in these species during the early breeding season (Phillips et al. 2004c).

5. 2 Methods

5. 2. 1 Tracking data

Tracking data used in this analysis were collected from GHA and BBA on Bird Island, South Georgia (54°00'S, 38°03'W), during the austral breeding seasons between 1992/93 and 2014/15 (for deployment details, see Phillips et al., 2004; Phalan et al., 2007; Scales et al., 2016). Hereafter, each breeding season is identified by the year in which the chicks fledge, e.g. 1992/93 as 1993. Locations were recorded using GPS loggers and Platform Terminal Transmitters (PTTs), with the mean interval dependent on GPS scheduling and number of fixes provided by the ARGOS satellite system (Additional file 1; Table S4. 1). Typically, birds with PTTs were also fitted with a 17 g radio transmitter attached to a plastic band on one tarsus which allowed exact arrival and departure times to be determined using a remote radio-receiver logger system (Televilt); otherwise, these were estimated from satellite fixes and visual observations during nest visits. In all cases, the total mass of devices including attachments was less than the 3% threshold of body mass beyond which deleterious effects are more common in oceanic seabirds (Phillips et al. 2003).

Chicks have been ringed annually since the 1970s, and the majority of the population in intensive study colonies on Bird Island is of known age. The sex of all birds (or their partners) was either determined from records of observed copulatory position, pre-laying attendance pattern, or using DNA extracted from a blood sample (Fridolfsson & Ellegren 1999) . Birds of known sex but unknown age were assigned a conservative minimum age of 8 years (BBA) or 10 years (GHA) when first ringed as breeding adults (Tickell 2000). Trips by these particular birds were only included in the analysis if their age when tracked exceeded

the average age at which senescence in breeding success is apparent in the study populations (Froy et al. 2017).

Individual trips were processed using an iterative forward/backward-averaging filter to remove any locations which required sustained flight speeds above 90 $km.h^{-1}$ [58]. Seven additional locations missed by the filter were later removed following visual examination of the tracks. Five tracks were incomplete because the device battery failed during the trip. Visual inspection indicated that this occurred during the outward portion of the trip in three instances, and during the return trip in two others. The former were excluded as no trip metrics could be calculated, and the latter were deemed 'near-complete' and included in further analyses. Finally, one trip that lasted for less than 6 hours was also excluded as it is likely that the adults were close to the colony and did not forage during that time (Weimerskirch et al. 1997b; Phillips et al. 2003).

As different devices and scheduling were used in different years (Additional file 1; Table S4. 1), the processed tracks were interpolated to 30 minute intervals (close to the mean for all recorded trips) using function 'redisltraj*'* in package 'adehabitatLT'(Calenge 2006). As very few individuals of known age (7%) were tracked for multiple trips, one trip was chosen at random for those birds. Data from the post-brood chick-rearing stage were excluded as the sample size for birds of known or minimum age was insufficient for further statistical analysis (4 trips). The final sample size was 51 tracks from the incubation stage (35 BBA and 16 GHA) and 107 tracks from the brood-guard stage (69 BBA and 38 GHA), collected between 1997 and 2015 from birds ranging between 10 and 45 years of age.

Immersion data were available in 2002, 2008, 2010 and 2015 for BBA and in 2003, 2010 and 2012 for GHA. These were collected using loggers with two different sampling protocols. Lower-resolution loggers (Mk IIa-V; British Antarctic Survey [BAS]) tested for saltwater

immersion every 3 s, storing the sum of positive tests every 10 minutes as a value ranging from 0 (continuously dry) to 200 (continuously wet). Higher-resolution loggers (GLS C-250 Intigeo; Migrate Technology Ltd, Cambridge, UK) also tested for immersion every 3 s, but recorded the time of transition between wet/dry states that lasted ≥ 6 s, providing the timing and duration of flights and landings, and consequently a more accurate indication of albatross activity throughout a given subset of foraging trips. Data from both loggers were used to calculate the proportion of the trip spent dry (in flight) versus wet (on the water). Immersion data were matched to corresponding GPS and PTT locations, providing data on at-sea activity for 44 tracks from the incubation (29 BBA and 15 GHA) and 86 tracks (54 BBA and 32 GHA) from the brood-guard stage. All data manipulations and analyses were conducted in R ver. 3.5.1 (R Core Team 2020).

5. 2. 2 Trip characteristics and activity pattern analysis

Depending on data availability, the following metrics were calculated for each foraging trip: (1) trip duration (days); (2) maximum range (maximum distance reached from colony in km), calculated using function 'homedist*'* in package 'trip' (Sumner 2016), (3) latitude at maximum distance from colony, (4) landing rate (wet events per hour), calculated as the total number of wet-dry transitions, (5) mean wet bout duration (minutes), and (6) wet time (proportion of total trip spent on the sea surface). Variables (4) and (5) were only available from high-resolution loggers. Variables (4), (5) and (6) were calculated separately for daylight and darkness as these albatross species are predominantly diurnal feeders (Phalan et al. 2007), using the function 'crepuscule*'* in package 'maptools' to determine the timing of civil twilight (when the sun is 6 degrees below the horizon, Bivand & Lewis-Koh 2017). 'Day' (daylight including twilight) or 'Night' were assigned accordingly. As there were only high-resolution immersion data for six GHA, metrics (4) and (5) were only investigated in BBA.

The relationships between these metrics, and age ('Age'), sex ('Sex'), species ('Species') and breeding stage ('Stage') of the birds, as well as the two-way interactions were investigated using linear models. 'Age' was modelled as a continuous variable, and each model tested for both linear and quadratic relationships between age and the various metrics to approximate the relationship previously found between age and breeding success at the population level in BBA and GHA (Froy et al. 2017). The models included two-level factors for 'Sex' (Male and Female), 'Species' (BBA and GHA) and 'Stage' (Incubation and brood-guard). Study year ('Year') was also included as an additive fixed effect to account for annual variation in environmental conditions, and was modelled as a seven-level factor for metrics (1)-(3) (1997, 2002, 2003, 2008, 2010, 2012, 2015), a three-level factor for metrics (4)-(5) (2008, 2010, 2015), and a six-level factor for metric (6) (2002, 2003, 2008, 2010, 2012, 2015). Metric (1) was square-root transformed, metrics (2), (4) and (5) were log-transformed, and metric (6) was logit-transformed to improve data spread. All possible models were ranked according to Akaike Information Criterion (AICc) values, and the most supported model(s) were considered as all models within 2Δ AICc of the top model (Burnham & Anderson 2004). Candidate models were excluded from this set if they were more complex variations of other candidate models with lower ΔAICc values (Arnold 2010). I did not consider models that contained age as a quadratic but not linear term (Age^2 without Age), or the interaction of the quadratic but not the linear age term with another linear predictor (e.g. Age^2: Stage without Age: Stage) for the models to remain well-formulated (Peixoto 1987; Berman et al. 2009). To prevent overfitting, all possible models were ranked in a second instance according to Leave One Out Cross Validation (LOOCV), and the top models were compared with those ranked according to AICc values (Lever et al. 2016).

5. 2. 3 Behavioural classification

Landings derived from immersion data are often used to identify foraging bouts in albatrosses (Phalan et al. 2007; Scales et al. 2016), as take-offs are energetically costly, and immersion events are likely to indicate prey capture attempts (Shaffer et al. 2001). As immersion data were not available for all trips, the Expectation Maximization binary Clustering (EMbC) algorithm was used to identify foraging bouts that were modelled in the subsequent habitat analysis. EMbC is a robust, non-supervised multi-variate clustering algorithm leading to meaningful local labelling of tracking locations based on the speed and turning angle obtained from successive locations (Garriga et al. 2016). The population-level analysis tool 'binClstStck' was used to analyse all tracks, and locations were classified according to four different clusters of high (H) and low (L) values of speed and turning angle. Clusters 2 and 4 were merged, grouping both low and high speeds at high turning angles (LH and HH), and resulting clusters were interpreted as follows: (1) LL as 'Resting', (2) LH and HH as 'Foraging', and (3) HL as 'Transit' (following Louzao et al. 2014). The plausibility of the EMbC behavioral clustering was verified by summarizing the landing rate and wet time during each state for all trips with immersion data (Additional file 1; Figure S1 and Table S4. 2).

5. 2. 4 Habitat preferences and oceanographic data

The habitat preferences of tracked BBA and GHA were investigated by comparing the environmental characteristics at the locations of foraging bouts with those in the areas that were available (use-availability) using binomial generalized additive models (GAMs), which allow for non-linear relationships between animals and the environment (Wood 2006; Aarts et al. 2008). Available areas were determined by generating 50 time-matched pseudo-absence points for every foraging bout location classified using EMbC by randomly rotating the foraging bout location around the study colony (Bird Island) to take movement

constraints into account (Wakefield et al. 2011). Pseudo-absences were re-generated if they intersected with land.

Environmental predictors (summarized in Table 5. 1) were selected as proxies of oceanographic and topographic features known, or hypothesized to be of importance for habitat selection in oceanic seabirds (Xavier et al. 2003; Phillips et al. 2006; Wakefield et al. 2011; Haug et al. 2015; Scales et al. 2016): (1) ocean floor depth (DEPTH - indicative of productive bathymetric areas such as shelf-breaks, seamounts and upwelling, GEBCO 2008), (2) sea surface temperature (Reynolds et al. 2007; SST - indicative of water masses, OISSTV2 2018), (3) chlorophyll α concentration (CHL - indicative of primary productivity, CMEMS 2018a), (4) eddy kinetic energy (EKE), and (5) sea level anomaly (SLA), indicators of mesoscale turbulence (CMEMS 2018b), (6) wind speed (Zhang et al. 2006; WIND - linked to movement costs and prey availability, NOAA 2018). All environmental datasets were accessed in 2018. Three further variables were calculated using function 'focal' in package 'raster': (7) depth slope (DEPTH SD; indicative of topographic features), (8) SST gradient (SST SD; a proxy for thermal fronts), (9) Chl gradient (CHL SD; another proxy for fronts), and (10) tracking year was included as a fixed effect ('Year'). All variables were downloaded as daily composites and resampled to 0.25°, corresponding to the coarsest scale of all datasets; using bilinear interpolation, recommended for continuous data (Patil et al. 2012). All environmental data as well as the location data were projected using the Lambert Conformal Conic projection centered at 37°W and 54°S (EPSG:3762), to limit distortion. Mean covariate values at the location of each foraging bout and pseudo-absence were then extracted using a 1.5km buffer with the function 'gBuffer*'* in package 'raster' to account for PTT location error (CLS Argos 2008). Locations with missing environmental values due to gaps in satellite observations (usually of wind speed) were excluded, resulting in a minimum

of 47 pseudo-absences per foraging-bout location. The four tracks from the breeding season of 1997 were not included in further habitat analysis as chlorophyll data were not available.

Table 5. 1: List of variables used in habitat analysis.

Variable	**Abbreviation**	**Source**	**Temporal resolution**	**Spatial resolution**
Bathymetry	DEPTH	GEBCO		0.02°
Bathymetric gradient	DEPTH SD	Calculated as standard deviation of Depth using function 'focal' in package 'raster'		0.02°
Sea surface temperature	SST	NOAA OI SST V2 High-resolution blended dataset	1 day composite	0.25°
Sea surface temperature gradient	SST SD	Calculated as standard deviation of SST using function 'focal' in package 'raster'	1 day composite	0.25°
Eddy kinetic energy	EKE	Copernicus global ocean gridded L4 sea surface heights and derived variables reprocessed	1 day composite	0.25°
Sea level anomaly	SLA			
Wind speed	WIND	NOAA blended sea winds	1 day composite	0.25°
Chlorophyll a concentration	CHL	Copernicus global ocean chlorophyll L4	1 day composite	0.04°
Chlorophyll a concentration gradient	CHL SD	Calculated as standard deviation of Chl using function 'focal' in package 'raster'	1 day composite	0.04°

Predictor variables were checked for collinearity by calculating all pairwise Spearman rank correlation coefficients. CHL and CHL SD were highly correlated (>0.6), and so two models were run with each predictor and compared using AIC. The model with CHL resulted in the lowest AIC value, and thus was interpreted as the better fit.

Separate models were constructed for different classes of birds because of computational demands and difficulties of interpreting high-order interactions. Initial models testing for interactions between species and breeding stage were significant, so the full model was split into four components, by species (BBA vs. GHA) and breeding stage (Incubation vs. Brood-guard). Using methods similar to Žydelis et al. (2011), the effect of different numbers of pseudo-absences was tested on the performance of these four models. Each individual model contained smoother splines for the environmental variables as well as for interaction of these variables with age. Smoothers were produced using cubic regression splines with shrinkage which penalize variables during fitting to reduce over-parameterization, and *k* was set to a maximum of 4 knots to reduce over-fitting (Wood 2006). A set of models consisting of all observed tracks and varying numbers of simulations (up to 47) per individual found that both the χ^2 for each parameter and the area under the receiver operator curve (AUC) stabilized around 20-30 pseudo-absences per individual. Consequently, 30 pseudo-absences per observed track were chosen for subsequent analysis (Additional file 1; Figure S2).

The inclusion of a random intercept for individual ID can help control for variability in response to the environment; however, model selection and inference in large datasets are computationally demanding within the mixed effects framework (Wood 2006; Aarts et al. 2008). The best minimal models were thus determined by forward selection using *k*-fold validation, testing the goodness of fit of each individual, in turn, against the prediction based on the other individuals (Wakefield et al. 2011; Carneiro et al. 2016). Model selection was based on the predictive ability of the models using Area Under the Curve (AUC) averaged across the *k* sets of results (i.e. individuals) using the 'pROC' package (Robin et al. 2011; Raymond et al. 2015). AUC values of 0.5-0.7, 0.7-0.9 and >0.9 represent poor, reasonable and very good model performances, respectively. The forward selection procedure consisted initially of fitting all possible single environmental predictors with and without the age-

interaction and ranking these models according to AUC. The best ranking model was chosen, and then each of the remaining predictors was added in turn (with and without the age interaction) and the best model among this new set was then retained if the AUC increased significantly. This process was repeated until there was no longer a significant increase in AUC between two models based on paired *t*-tests. Habitat preference models were fitted separately for the incubation and brood-guard stages for both BBA and GHA.

5. 3 Results

Tracked BBA and GHA foraged over a wide area around Bird Island during the incubation and brood-guard stages (ranging from 38-65°S and 73°W-5°E; Figures 5.1 & 5.2), and showed age-related variation in foraging trip characteristics, activity patterns and habitat preferences (See Additional file 1, Tables S4. 3 and S4. 4, for full model selection and parameter estimates).

5. 3. 1 Age-related variation in trip characteristics

The age of BBA and GHA had a strong effect on the duration of their foraging trips, as evidenced by the age terms (Age, Age^2, Age: Stage, Age^2: Stage and Age: Species) retained in the average of the top models (Table 5. 2, Figure 5. 3a). During the incubation stage, the duration of foraging trips of both species declined in early adulthood until age 26 years (BBA: modelled change of -4.3 [36%] and -4.6 [34%] days in males and females respectively, GHA: modelled change of -1.4 [13%] and -1.6 [13%] days in males and females respectively), although this relationship was not as pronounced in GHA because fewer young birds were tracked during incubation (only 6 GHA were <26 years and all 6 were ≥ 18 years). Foraging trip duration then increased in both species as the birds reached old age (BBA: modelled change of +2.1 [26%] and +7.5 [83%] days in males and females, respectively, GHA: modelled change of +6.6 [71%] and +7.1 [69%] days in males and females, respectively). Although this trend may be driven in BBA by the two oldest birds, the

top two models ranked according to LOOCV contained the same predictor variables as those ranked according to AICc, suggesting outliers had little influence on model selection (Tables S4. 3 and S4. 5). The quadratic relationship with age was less apparent during the brood-guard stage, when mean trip durations were considerably shorter (by ~ 7.6 days). Overall, GHA took slightly longer trips on average than BBA (by ~ 1.0 days), and females took slightly longer trips than males regardless of species and stage (by ~ 2.2 days).

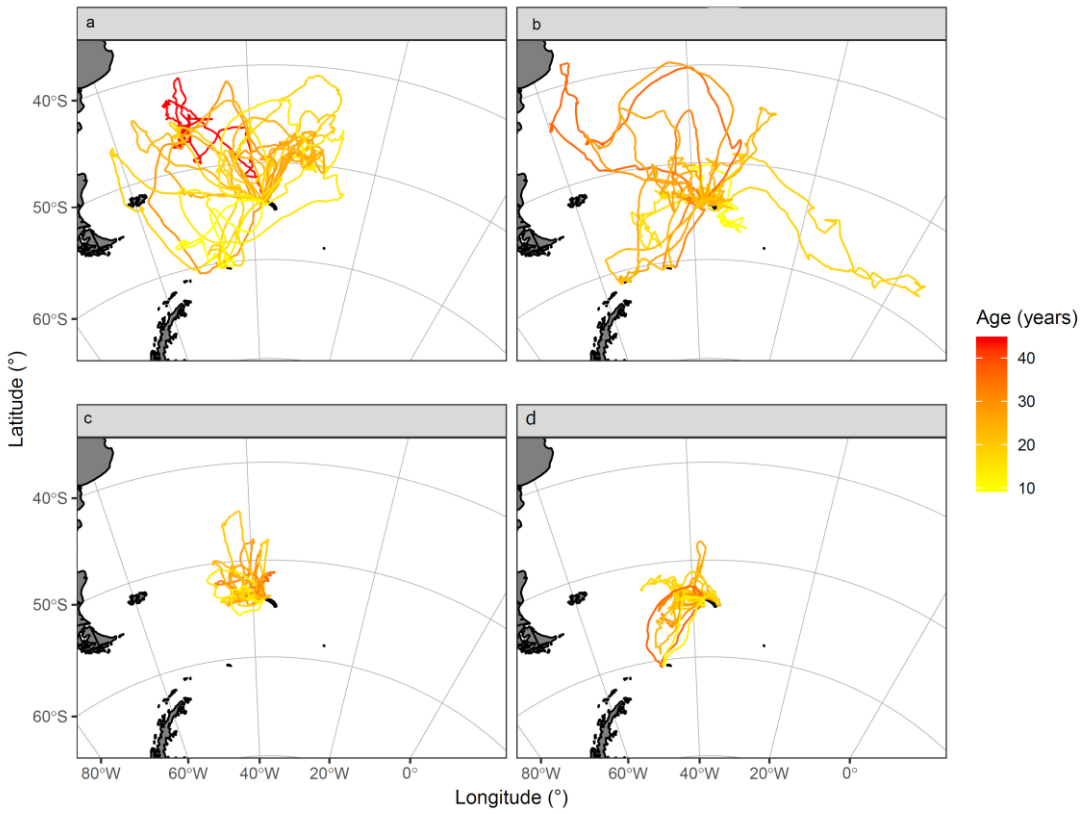

Figure 5. 1: Distribution of foraging trips from all aged and sexed black-browed albatrosses breeding at Bird Island, South Georgia, during the incubation and brood-guard stages in austral summers 1996/97 to 2014/15. 'a' incubating females (17 tracks), 'b' incubating males (18 tracks), 'c' brood-guard females (20 tracks) and d brood-guard males (49 tracks).

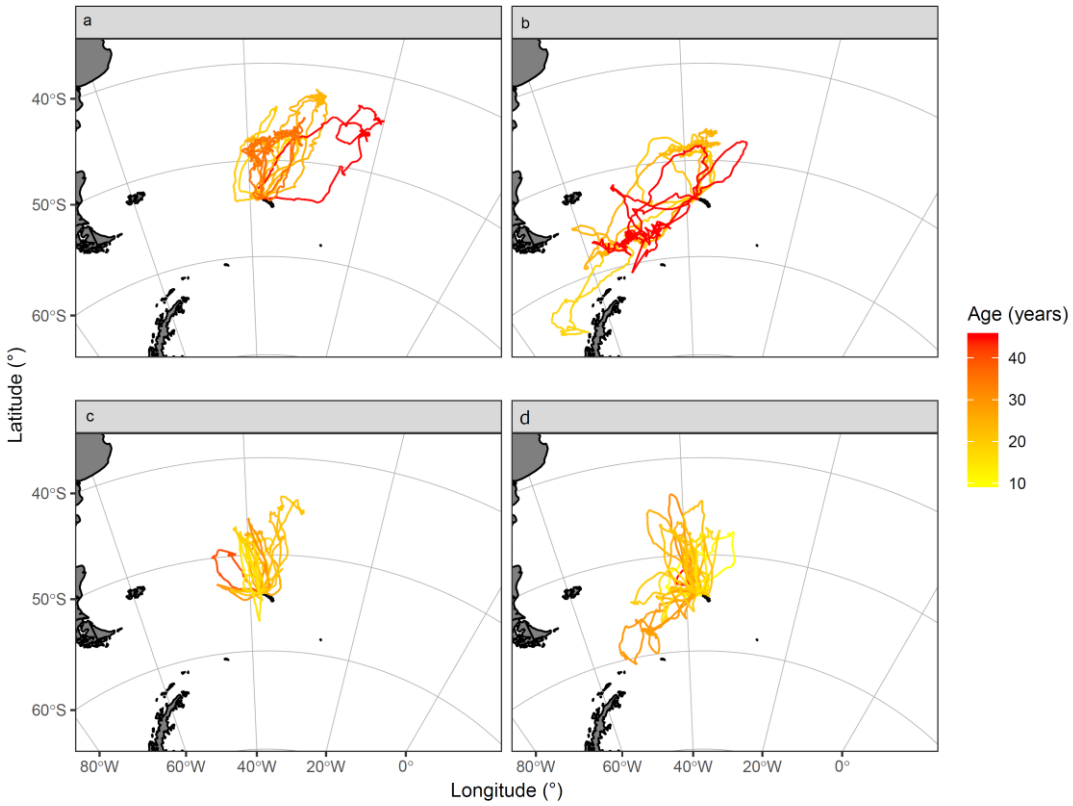

Figure 5. 2: Distribution of foraging trips from all aged and sexed grey-headed albatrosses breeding at Bird Island, South Georgia, during the incubation and brood-guard stages in austral summers 2002/03 to 2011/12. 'a' incubating females (9 tracks), 'b' incubating males (7 tracks), 'c' brood-guard females (13 tracks) and 'd' brood-guard males (25 tracks).

Table 5. 2: Effects of age, sex, stage, species and year on trip characteristics and activity patterns of black-browed and grey-headed breeding at Bird Island, South Georgia. 'x' indicates terms retained in the average of the best-supported models for each response variable (full model selection and parameter estimates are listed in Tables S4. 3 and S4. 4).

		Predictor variables															
Response variable	**n**	Intercept	Age	Age^2	Sex	Stage	Species	Year	Age: Sex	Age^2: Sex	Age: Stage	Age^2: Stage	Age: Species	Age^2: Species	Sex: Stage	Sex: Species	Stage: Species
Trip duration (days)	158	x	x	x	x	x	x				x	x	x				
Max range from colony (km)	158	x			x	x	x	x								x	
Latitude at max range (°)	158	x	x	x	x	x	x				x	x	x		x		x
Landings.hr^{-1} in daylight[a]	66	x	x		x			x	x								
Landings.hr^{-1} in darkness[a]	64	x						x									
Wet bout length in daylight (mins)[a]	66	x	x		x												
Wet bout length in darkness (mins)[a]	64	x						x									
Prop daylight wet (%)	130	x					x	x									
Prop darkness wet (%)	128	x			x	x	x	x									

[a] Species was not included in the model for these two metrics as sample size was very small for GHA.

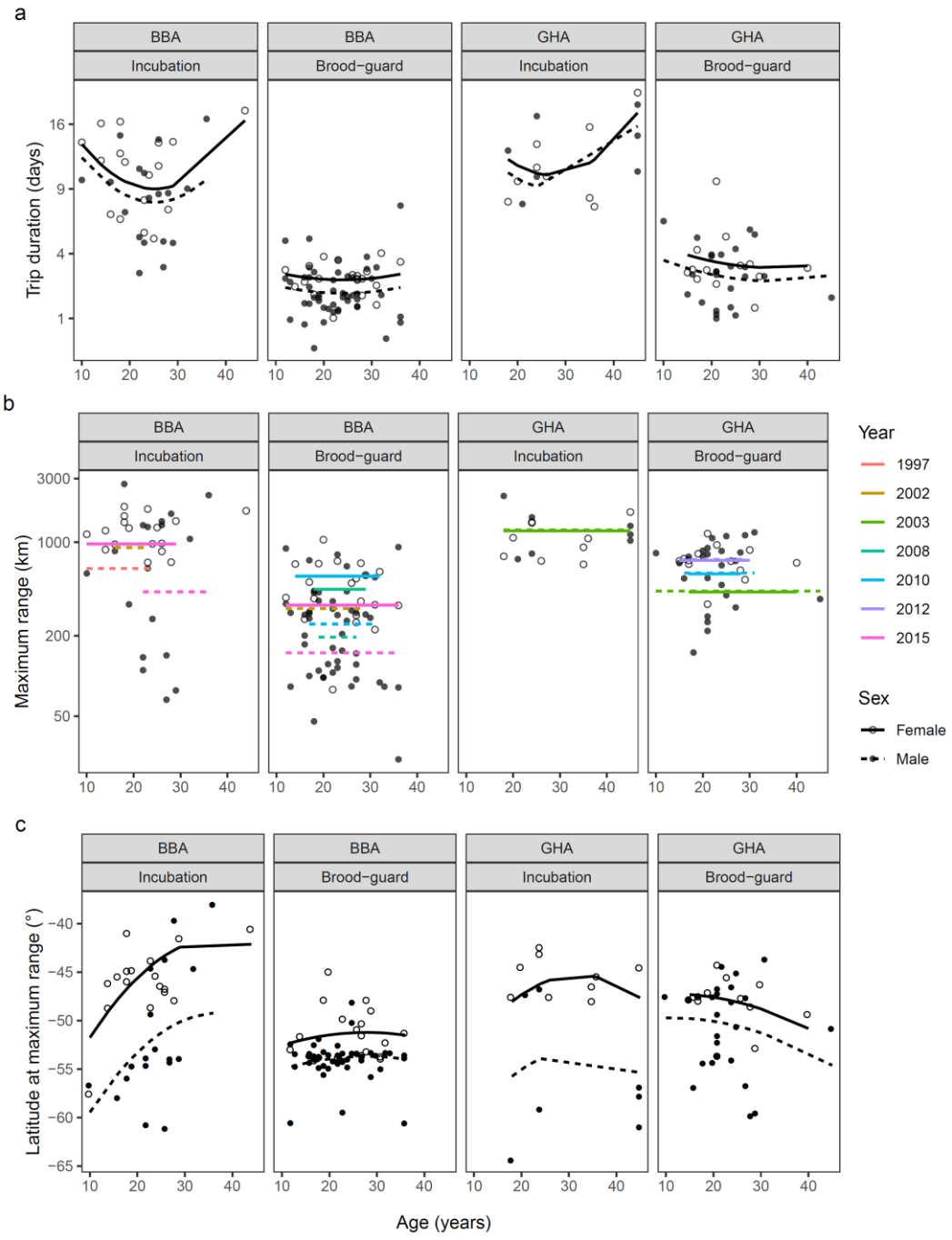

Figure 5. 3: Relationship between age and foraging behaviour for male (open circles) and female (closed circles) black-browed (BBA) and grey-headed (GHA) albatrosses during the incubation and brood-guard stages. Regression lines indicate the fitted values of the average of the most supported models for each response variable. Where a significant effect of sex was found, males (solid) and females (dotted) are shown with separate lines. Horizontal lines indicate no age effect but a significant sex effect. Values

of transformed response variables (a & b) are back-transformed on the y-axis but the scale of the transformation is retained.

Age was also included as a quadratic term in the top models explaining the latitude reached by birds at maximum distance from the colony (Table 5. 2, Figure 5. 3c), suggesting age-related segregation in foraging distributions, and warranting further investigation of habitat preferences. Incubating BBA foraged at progressively northerly latitudes with increasing age (increase in 10.2° of latitude in males aged between 10-36 years and in 9.6° of latitude in females aged between 10 and 44 years). GHA during incubation showed very little age-related variation in latitude but foraged at progressively southerly latitudes with increasing age during the brood-guard stage (decrease in 4.9° of latitude in males aged between 10 and 45 years, and 3.5° of latitude in females aged between 15 and 40 years), whereas BBA of different ages foraged at similar latitudes during brood-guard, usually close to Bird Island between -55° and -56° S (Figure 5. 3c). Overall, females foraged at more northerly latitudes (by ~ +4.6°) than males, especially during incubation (Figure 5. 3c; the difference in the latitudes reached by females and males increased during the incubation stage by ~ 4.4°). GHA foraged on average at more northerly latitudes than BBA, especially during the brood-guard stage (by ~ +3.5°).

Age did not, however, influence the maximum range of birds during foraging trips (Table 5. 2, Figure 5. 3b). As expected, all birds foraged further afield during the incubation stage (by ~ 517 km on average). Male BBA foraged on average 392 km closer to the colony than female BBA regardless of stage, but there was less difference (~143 km) between the maximum ranges of male and female GHA. This metric also varied significantly between study years; by 523 km and 305 km between the lowest and highest average yearly ranges for BBA and GHA, respectively.

5. 3. 2 Age-related variation in activity patterns

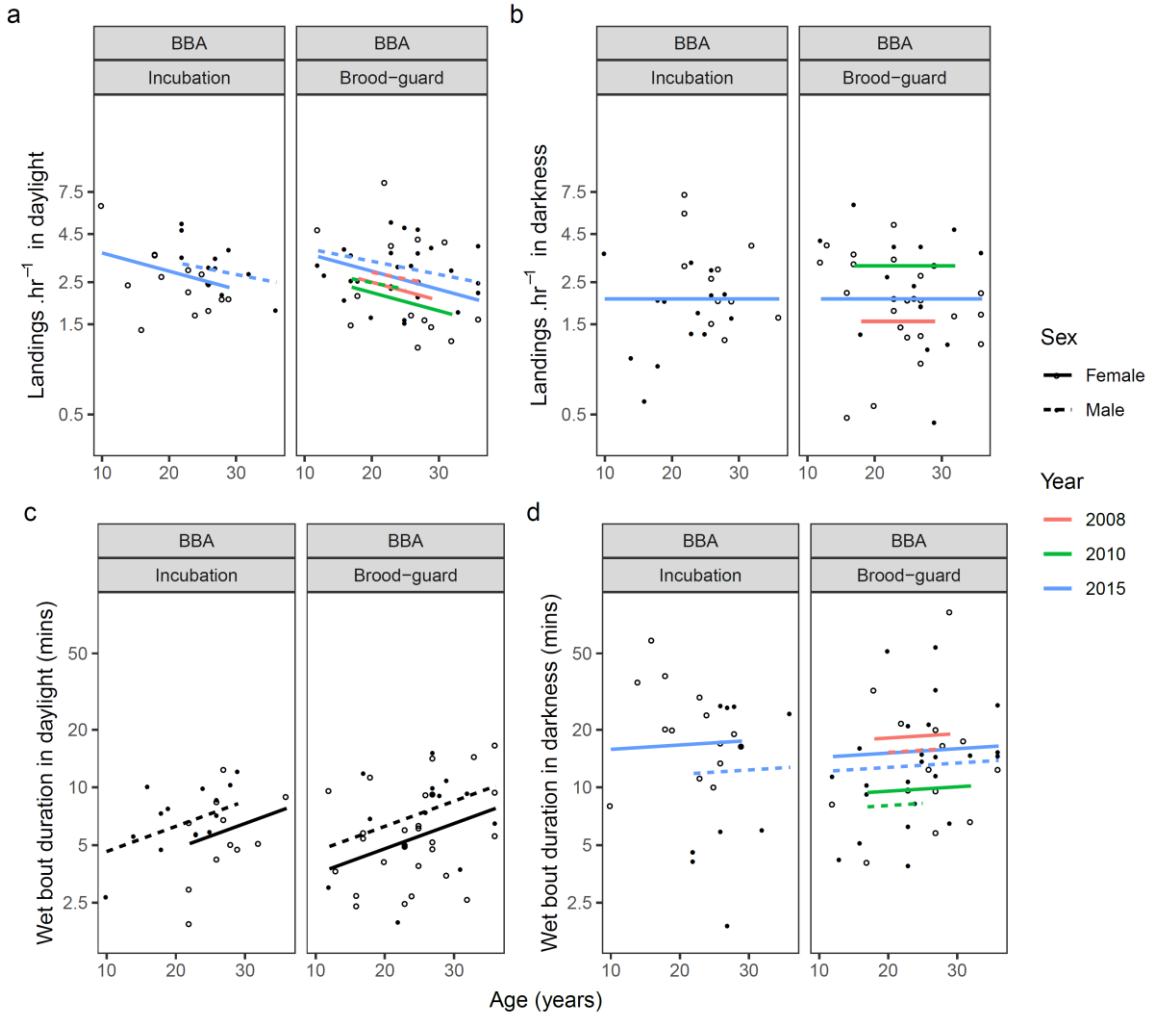

Figure 5. 4: Relationship between age and high-resolution activity metrics for male (open circles) and female (closed circles) black-browed (BBA) albatrosses during the incubation and brood-guard stages. Regression lines indicate the fitted values of the average of the most supported models for each response variable. Where a significant effect of sex was found, males (dotted) and females (solid) are shown with separate lines. Horizontal lines indicate no age effect but a significant sex effect. Values of transformed response variables (a-d) are back-transformed on the y-axis but the scale of the transformation is retained.

Age was retained in the top models describing landing rate and mean wet bout duration of BBA in daylight (Table 5. 2, Figure 5. 4a and c). With age, BBA landed less often on the water (modelled change of -1.2 landings.hr^{-1} [32%] and -1.6 landings.hr^{-1} [44%] between 10 and 36 years old for males and females respectively; Figure 5. 4a). The third most-supported model for this metric suggested a faster decline in landing rate with increasing age in female BBA, but this effect was deemed minimal as it was only included in one of the top three models (Additional file 1; Table S4. 3). BBA also spent increasing time on the water between landings (modelled change of +3.2 minutes [55%] between ages 12 and 36 years, and +5.5 minutes [52%] between ages 10 and 36 years for males and females, respectively). This trend was apparent for both breeding stages, but females spent slightly more time on average on the water in daylight than males (by 1.4 minutes). Age, however, had little bearing on these metrics during darkness. Instead, mean landing rate and wet bout duration in darkness varied strongly between study years (Table 5. 2). BBA were the least active in darkness in 2008, landing less often (by ~1.5 landings.hr^{-1}) and spending more time on the water between landings (by ~ + 7.8 minutes) than in 2010, the year when activity was highest. Age, stage and sex effects were included in the third top model explaining variation in wet bout duration during darkness, but as these terms were not included in the other two models, their effects were again deemed minimal (Additional file 1; Table S4. 3).

The overall proportion of the foraging trip spent wet during daylight and darkness varied between species and study year (Table 5. 2, Figure 5. 5a and b). BBA spent on average 2% more of their trips wet during daylight than GHA, regardless of sex and breeding stage (Figure 5. 5a). The reverse was true in darkness, during which GHA spent 19% more of their trip on average on the water than BBA (Figure 5. 5b). This was apparent regardless of sex and breeding stage during daylight (Figure 5. 5a, Table 5. 2). There was only weak evidence for an effect of these terms during darkness as they were not included in the top models as

ranked by LOOCV (Additional file 1; Table S4. 5). This activity metric fluctuated considerably between study years for BBA, especially during darkness (modelled 20% and 28% difference between the lowest and highest values in daylight and darkness, respectively). The variation among study years was less for GHA during daylight, but was comparable to that in BBA during darkness (modelled 12% and 25% difference between the lowest and highest values in daylight and darkness, respectively).

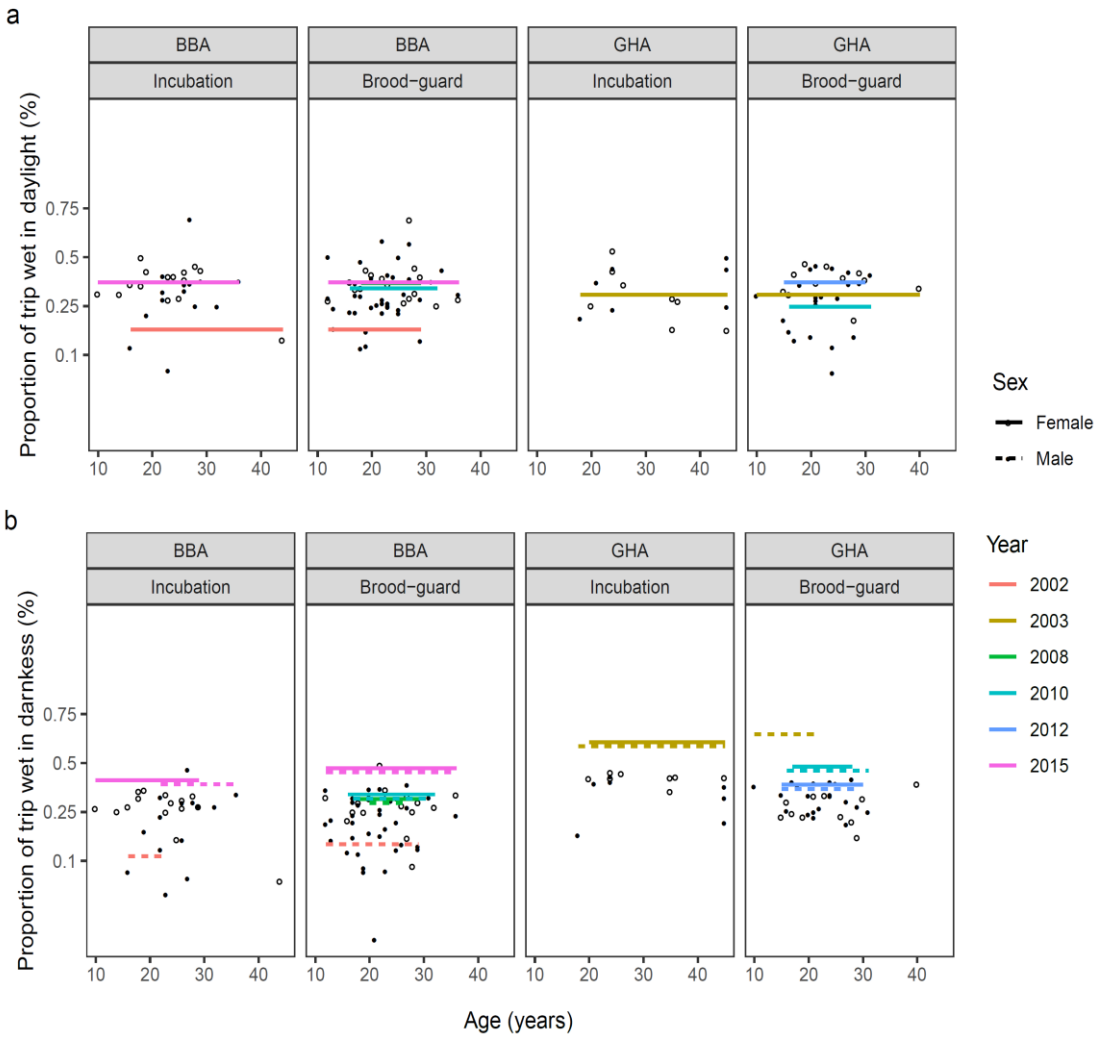

Figure 5. 5: Relationship between age and low-resolution activity metrics for male (open circles) and female (closed circles) black-browed (BBA) and grey-headed (GHA) albatrosses during the incubation and brood-guard stages. Regression lines indicate the fitted values of the average of the most supported models for each response variable.

Where a significant effect of sex was found, males (dotted) and females (solid) are shown with separate lines. Values of transformed response variables (a-b) are back-transformed on the y-axis but the scale of the transformation is retained.

5. 3. 4 Age-related variation in habitat preferences

There was evidence for age-specific habitat preferences in the models predicting the distribution of foraging bouts of GHA but not BBA (Table 5.3, Figures 5.6 and 5.7). The most important predictor of habitat use for GHA was 'SST' interacting with the 'SEX' and 'AGE' of the birds for both the incubation and brood-guard stages (Table 5.3, Figure 5. 6 a-d). Excluding the youngest (18 years) incubating male GHA, which foraged in cold waters off the Antarctic Peninsula (Figure 5. 6a; 0-5°C), model response contour plots indicated that during incubation, male and female GHA showed a progressive narrowing in temperature preference with increasing age (Figure 5. 6a and b). Indeed, younger birds of both sexes foraged indiscriminately across a wide range of SST (Figure 5. 6a and b; males: 2-20°C, females: 3-14°C), whereas older birds targeted specific habitats. Old males (40-45 years) avoided warmer waters to the north of South Georgia, preferentially foraging in colder southerly waters (Figures 5. 2 and 5. 6a; 0-6°C) and the oldest female (45 years) targeted an entirely separate foraging habitat to other females, to the north-west of the colony (Figure 5. 2 and 5. 6b; 5-8°C). During brood-guard, females similarly foraged within a narrowing temperature range with increasing age (Figure 5. 6d: 0-15°C in 15-30 years and 0-10°C in 35-40 years). This age-related shift in habitat preference was not as strong as in the incubation stage, presumably because movements and habitat choices were limited by the greater central-place constraint. In contrast, only young brooding male GHA showed a specific temperature preference, avoiding cold waters to the south of the colony (Figure 5. 2 and 5. 6c; >2°C).

Table 5. 3: Environmental predictor variables retained in the best models explaining the distribution of foraging bouts in black-browed albatrosses (BBA) and grey-headed albatrosses (GHA) during different breeding stages. Habitat preference models were constructed separately for both species and for the incubation and brood-guard breeding stages. An 'x' indicates terms retained in the best model for each combination of species and breeding stage. Where an 'x' is followed by a colon and either 'Sex', 'Age' or 'Sex: Age' indicates a two or three-way interaction of those terms with that particular environmental predictor variable. Mean Area Under the Curve (AUC) scores and standard deviations (sd) of those scores for each model are indicated in the final column. Values of 0.5-0.7, 0.7-0.9 and >0.9 represent poor, reasonable and very good model performance, respectively.

Model predictors	DEPTH	DEPTH SD	SST	SST SD	CHL	WIND	SLA	EKE	AUC (sd)
Dataset									
BBA Incubation			x						0.76 ± 0.11
BBA Brood-guard	x		x, SST: Sex						0.89 ± 0.08
GHA Incubation			x, SST: Sex: Age						0.76 ± 0.12
GHA Brood-guard			x, SST: Sex: Age						0.81 ± 0.08

The best models predicting the distribution of foraging bouts in GHA performed reasonably well, with AUC=0.76 and AUC=0.81 for the incubation and brood-guard stages respectively. However, the accuracy of the predictions when calculated separately for each individual varied more for the incubation stage, when the birds took longer trips, suggesting greater variability in their habitat preferences (AUC of 0.65-0.87) than during brooding (AUC of 0.73-0.89).

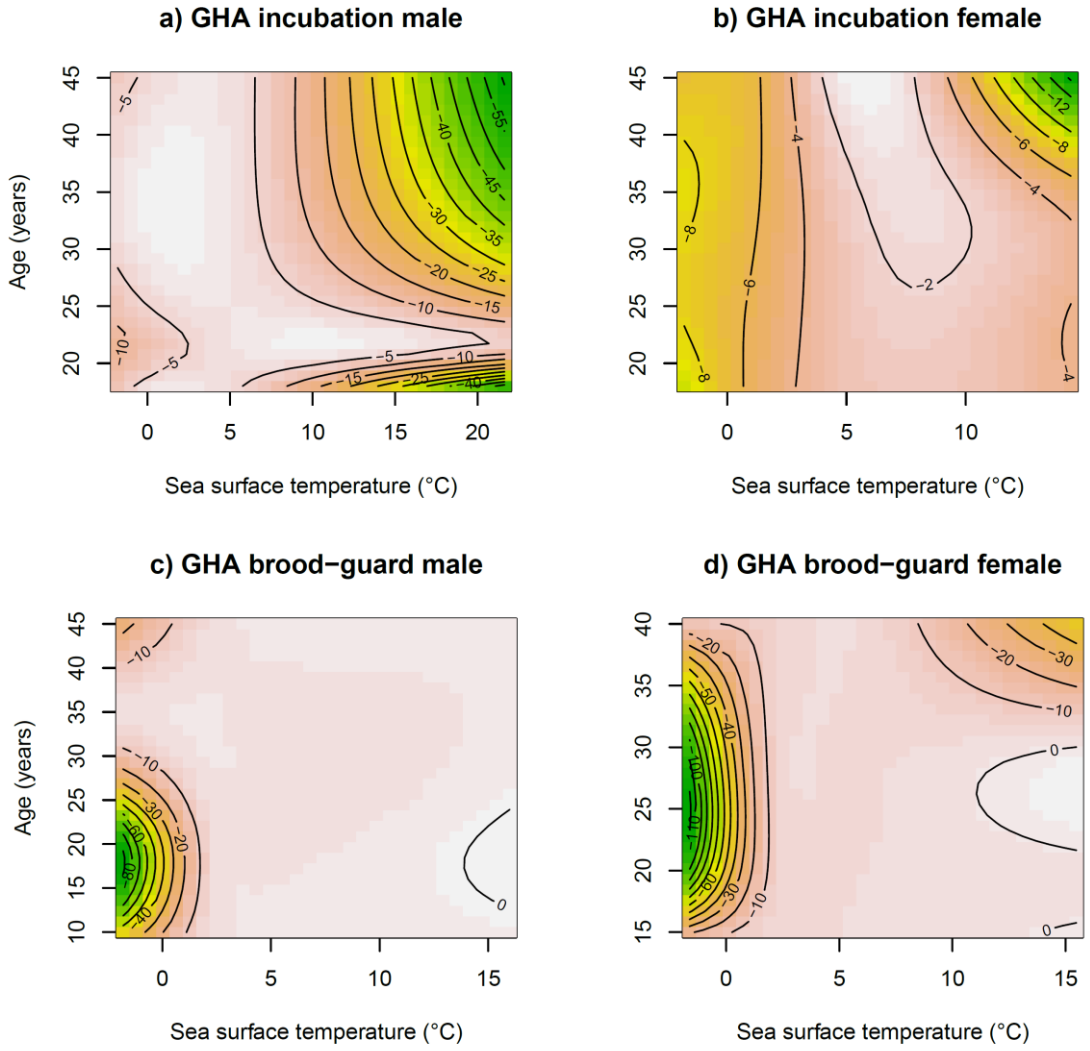

Figure 5. 6: Contour plots (a-d) of most important variables explaining the distribution of grey-headed albatrosses (GHA) foraging bouts during the incubation and brood-guard breeding stages. Probability of foraging bout occurrence for bird of different ages and values of sea surface temperature is represented by color (high probability of occurrence; red, low probability of occurrence; green).

The most important predictor of habitat use in BBA during the incubation stage was also 'SST' but without any interaction with sex or age. Model response curves indicated that probability of foraging was highest in warmer waters between 4 and 15°C (Figure 5. 7a) between the Antarctic Peninsula and Patagonian Shelf (Figure 5. 1a). 'DEPTH' was the most

important predictor of habitat use of BBA during the brood-guard stage, followed by the interaction of 'SST' and 'SEX'. Model response curves indicated that brooding BBA preferentially foraged in neritic waters close to the colony (Figure 5. 7b; the probability of foraging increased with decreasing depth). Female BBA preferentially foraged in waters spanning a wide range of temperatures (Figures 5. 1a and 5. 7c; 2-15°C) to the northwest of South Georgia, whereas males preferentially foraged in colder waters to the southwest (Figures 5. 1a and 5. 7c; <5°C).

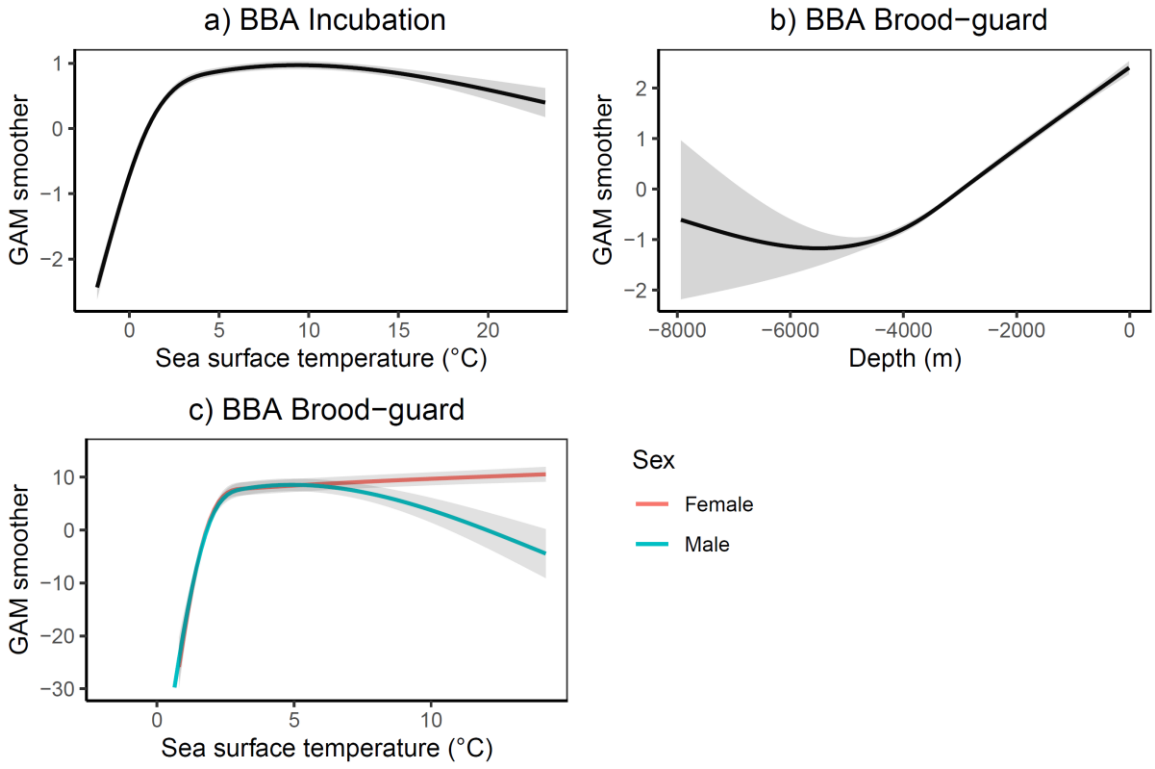

Figure 5. 7: Response curves (a-c) of most important variables explaining the distribution of black-browed albatross (BBA) foraging bouts during the incubation and brood-guard breeding stages. Sex is represented by color for females (red) and males (blue) in plot c. Standard errors of the responses from model outputs are shown in grey.

As with the models for GHA, the model of habitat preferences of BBA during brood-guard was more accurate than during incubation (AUC=0.76 and AUC=0.89, respectively), and

varied less for BBA during incubation than brood-guard when calculated separately for each individual (AUC between 0.65 and 0.87, and between 0.71 and 0.97, respectively).

5. 4 Discussion

This study found evidence of extensive age-related variation in the foraging behavior of two congeneric, long-lived seabirds; black-browed (BBA) and grey-headed (GHA) albatrosses, during the breeding season. As I hypothesized, young breeders of both species displayed age-specific patterns in terms of trip duration (BBA and GHA), latitudinal distribution (BBA and GHA) and foraging activity at sea (BBA), but in contrast to my expectations, so did old breeders of both species. As predicted, effects of age were most apparent during incubation; however, there was evidence of age-specific activity patterns in BBA and habitat preferences in GHA irrespective of breeding stage, whereas older GHA segregated at-sea from younger birds during the brood-guard stage only. These findings highlight the complex interaction between the changing degree of the central-place constraint and the intrinsic attributes of individual seabirds in shaping foraging behavior.

5. 4. 1 Age-related variation in foraging behavior in early adulthood

Naïve individuals show marked improvements in foraging performance during early life as they gain experience in how to move, navigate, locate prey and other skills (Wunderle 1991; Avens 2004; Russon 2006). Although many species of seabirds have a prolonged immaturity phase, individuals may require additional skills to forage successfully for both themselves and their young once they recruit into the breeding population (Haug et al. 2015; Clay et al. 2018).

Here, the foraging behavior of young breeders of botevidence of h albatross species differed initially from that of mid-age and old individuals (as seen in other species; Weimerskirch et al. 2005; Dukas 2008; Patterson et al. 2016; Lescroël et al. 2019). Foraging trips were longer

in young than mid-age BBA during the incubation stage, and they showed higher activity levels irrespective of breeding stage, landing more often and resting for less time on the water between landings. A previous tracking study at the Crozet Islands found that young (5-year-old) king penguins (*Aptenodytes patagonicus*) conducted longer trips than older individuals (9-year-olds), performed more dives (a proxy for foraging effort), and were less efficient at foraging (Vaillant et al. 2013). As albatrosses are under strong selection to forage efficiently during the incubation stage to minimize the risk of their partner deserting before they return, my results suggest that reduced foraging competency contributes to the lower reproductive success observed in young BBA breeding at Bird Island (Froy et al. 2017). It is difficult to verify this hypothesis without data on daily mass gain during trips or success rates of individual foraging bouts, but BBA recruit into the breeding population at a younger age than in other albatross species, and it seems likely they are still honing their skills in capturing, locating or handling prey (Wunderle 1991; Weimerskirch et al. 2005; Froy et al. 2017). Alternatively, BBA may need several breeding attempts to adapt to the new constraints imposed on foraging behavior by breeding, such as coordinating nest attendance with a mate, or competing for prey amongst high densities of conspecifics in waters around the colony (Weimerskirch & Lys 2000). Indeed, young BBA foraged at more southerly latitudes during the incubation stage but did not differ in habitat preferences from older birds, indicating they may avoid prey aggregations where competition is greatest, as seen in young wandering albatrosses (*Diomedea exulans*) (Bretagnolle 1993).

My analysis also suggested that young GHA took longer foraging trips than mid-age individuals during the incubation stage. This trend is to be interpreted with caution, however, as the sample of tracked birds was skewed towards older individuals (all birds were ≥ 18 years old and GHA generally recruit at 13 years old; Froy et al. 2017). As young GHA during incubation also had wider habitat preferences than older birds in terms of sea surface

temperature, the longer trips may have resulted from lower efficiency at locating profitable foraging habitats, as seen in young Cory's shearwaters (*Calonectris borealis*) (Haug et al. 2015). While it could be hypothesized that this behavior is representative of breeders in general (as the subset of tracked birds already had several years of breeding experience), my sample of brooding birds included very young breeders (10 years old was the minimum age), and these individuals had similarly wide habitat preferences. The increased severity of the central-place constraint during brood-guard did not constrain these preferences, and may explain lower breeding success in young GHA if they are unable to locate and deliver high-quality prey to their young (Daunt et al. 2001; Limmer & Becker 2009; Navarro et al. 2010).

Honing foraging skills over several breeding attempts may drive the within-individual improvement in breeding success observed in early adulthood in BBA and GHA (Froy et al. 2017), which could be tested by longitudinal tracking studies of individuals over several years. Alternatively, there may be selection for high-quality individuals with specific foraging strategies (short trip durations, low landing rate, more northerly distributions; Daunt et al. 2007b; Nevoux et al. 2007), or poor environmental conditions (via food scarcity) may disproportionally affect the foraging success of naïve individuals in certain years (Haug et al. 2015).

5. 4. 2 Age-related variation in foraging behavior in late adulthood

In late adulthood, in contrast to my expectations, GHA as well as BBA showed signs of age-related changes in foraging behavior, even in the absence of significant population-level reproductive senescence in BBA (Froy et al. 2017). Furthermore, the changes in certain foraging traits occurred at a later age than recorded population-level declines in breeding success, while other changes occurred progressively with age, suggesting there is a complex relationship between foraging and reproductive performance in these two species (Froy et al. 2017).

Foraging trip duration in incubation increased in GHA from age 26 onwards. This confirms the results of a previous study at Bird Island in the 2002/03 breeding season which found that old (≥ 35 years old) males took longer trips than mid-aged (≤28 years old) males (Catry et al. 2006). These older male GHA also showed reduced foraging and breeding performance, suggesting they may be constrained by some degree of physical deterioration in old age (Curio 1983). Benefiting from a larger dataset, I also found that female GHA took longer trips with increasing age. Differences between age groups in performance might only be apparent when conditions are sub-optimal, and it could be hypothesized that females encountered particularly unfavorable conditions at sea in 2011/12 compared to 2002/03 (Sydeman et al. 1991). Older incubating birds of both sexes also showed a progressive change in preferred foraging habitat with increasing age in that they targeted a narrowing range of sea surface temperatures. This pattern could indicate a further increase in foraging efficiency with age, with birds targeting predictably productive areas learned through experience (Haug et al. 2015). However, old incubating GHA did not forage within areas particularly rich in their preferred prey (the squid, *Martialia hyadesi*) (Xavier et al. 2016) and habitat selection in old individuals of a number of taxa is mediated by age-related increases in the incidence of disease or injury (Montgomery et al. 2013; Jaeger et al. 2014; Hayward et al. 2015). Indeed, it has been suggested that senescent female Soay sheep (*Ovis aries*) have smaller home ranges of lower quality as a result of competitive exclusion by younger conspecifics, and that male wandering albatrosses forage progressively further south with increasing age to reduce foraging costs by flying in windier areas (Lecomte et al. 2010; Hayward et al. 2015; Froy et al. 2015) . These two theories may explain the behavior seen in GHA in my study, especially as the oldest birds foraged in more southerly and windier areas during the brood-guard stage.

Increased foraging trip duration in older BBA also suggests they experience senescence in foraging performance, as hypothesized for GHA. BBA do not show reproductive senescence, however, and hence they may be able to maintain high foraging efficiency in spite of potential physiological decline. Similarly, old Brünnich's guillemots (*Uria lomvia*) did not differ in dive behavior from young birds, but had lower blood oxygen stores, resting metabolic rate and thyroid hormone levels (Elliott et al. 2014). In accordance with the so-called 'restraint' hypothesis (Williams 1966), taking longer trips may be an energy-saving tactic, which would allow BBA to offset physiological deterioration, and maintain a consistent level of foraging efficiency and hence reproductive success into old age. BBA also showed a progressive decrease in foraging effort with increasing age, landing less often and resting for longer on the water between landings, which may reflect this energy-saving tactic. Indeed, while this trend could imply that old birds are simply more efficient at foraging, old (20+ years) wandering albatrosses tracked from Bird island during the non-breeding season that landed more often on the water were less likely to breed successfully the following year (Clay et al. 2018). The study that investigated reproductive aging on Bird Island included few BBA older than 40 years of age (Froy et al. 2017), and it is possible that the change I observed in foraging behavior in old age eventually affects average reproductive success, but only in very old birds.

It is noteworthy that progressively longer foraging trips during incubation were apparent from the same point in late adulthood in both species, even though BBA are annual breeders and hence senescence should in theory commence earlier and develop more quickly than in GHA, which breed biennially (Tickell & Pinder 1975; Jones et al. 2008). Further research may reveal whether this difference indicates a true deviation from life-history theory or is unrelated to breeding success. BBA taking shorter trips may have been exposed to high incidental mortality in fisheries operating historically around South Georgia, resulting in the

selective disappearance of birds that take shorter foraging trips (Dalziell & Poorter 1993). Alternatively, there may be an effect of the environment experienced by these birds on their aging trajectories, considering that BBA and GHA forage largely in different areas during breeding, overlap very little at sea during the nonbreeding season and were tracked in separate years (Reznick et al. 2000; Phillips et al. 2004c). Environmental effects may also explain why wandering albatrosses breeding at Bird Island showed no obvious changes in foraging behavior with age in spite of age-related variation in breeding success (Froy et al. 2015).

5. 4. 3 Other drivers of foraging behavior during the breeding season

Within species, the intensity of aging often varies according to sex, in association with the strength of sexual selection, and the cost of producing or maintaining sexually selected traits or behaviors (Clutton-Brock & Isvaran 2007; Maklakov & Lummaa 2013; Adler & Bonduriansky 2014). I found no strong evidence for an interaction between the sex and age of individual GHA and BBA on their foraging behavior, despite the sexual dimorphism in wing area and wing loading in both species, and the higher chick provisioning rate of male BBA (Huin 2000; Phillips et al. 2004c). However, females of both species did make longer foraging trips during both breeding stages, and female BBA rested for longer on the water between foraging bouts than males during daylight. These trends suggest that females of both species allocate more effort to self-maintenance, as seen for example in female little auks (*Alle alle)* which take long self-feeding trips to replenish body reserves used during egg production (Welcker et al. 2009b). This behavior may enable females of both species to achieve a longer reproductive lifespan, whereas males may pay a physiological price for maintaining higher levels of foraging effort (Carranza et al. 2004; Froy et al. 2017). Otherwise, females of both GHA and BBA foraged at more northerly latitudes than males

during incubation, in keeping with previous research which attributed this spatial segregation to differences in flight performance (Phillips et al. 2004c).

BBA showed no age-specific habitat preferences, but instead preferentially foraged within a wide range of relatively warm sea surface temperatures during both breeding stages. Probability of foraging with respect to SST peaked at around 3°C and remained constant thereafter in females, but decreased in males in waters above 5°C during the brood-guard stage. This difference in preference may indicate that male and female BBA have differing nutritional demands that induce them to target prey that associate with particular temperature regimes (as suggested for northern gannets (*Morus bassanus*); Lewis et al. 2002). Alternatively, it may relate to the more northerly distribution of female BBA during brood-guard for other reasons (e. g. related to wind regime preferences; Phillips et al. 2004c). Both sexes also preferentially foraged in shallow waters, most likely as they were constrained to remain close to the colony during this breeding stage (Ricklefs 1983). My analyses did not find preferences for quite the same suite of environmental covariates that predicted habitat use in previous studies of both BBA and GHA, for instance eddy kinetic energy or chlorophyll concentration (Wakefield et al. 2011; Scales et al. 2016). However, my sample differed from those studies in that it only included birds of known age and sex, and there is always considerable individual and annual variability in preferred foraging habitats (Xavier et al. 2003; Phillips et al. 2017).

There were no obvious age-specific patterns in terms of activity budgets. BBA spent a larger proportion of time on the water during the day, and a smaller proportion on the water at night than GHA. These findings match previous research suggesting a degree of specialization in feeding behavior between these two species, perhaps as a result of competition (Phalan et al. 2007). In addition, activity metrics, as well as maximum foraging range, varied between years in both species indicating these birds show flexibility in response to varying

environmental conditions and, consequently, distribution or availability of prey. This differs from previous research suggesting that the smaller albatrosses (*Thalassarche* and *Phoebetria* species) have similar overall energy budgets (Weimerskirch & Guionnet 2002). Finally, additional fine-scale activity data is needed for GHA of known age, as there may be age-specific changes that I was unable to detect.

5. 4. 4 Conclusion

Here I demonstrated that several aspects of the foraging behavior of black-browed and grey-headed albatrosses breeding at South Georgia were related to age. While this study was purely cross-sectional, and inferences about the consequences of foraging behavior for fitness could not be tested at the individual level, it nevertheless identified some clear patterns at the population-level. As more studies seek to better link tracking data to physiology and life-history decisions and events of individuals, there will be increasing opportunity to ask complex questions regarding relationships between age-specific variation in behavioral traits and multiple aspects of fitness (breeding success, timing of breeding, chick growth rates etc.; Crossin et al. 2014). These questions are of fundamental ecological and evolutionary interest (Roach & Carey 2014) and are likely to have important consequences for the population dynamics of these threatened albatrosses as well as other species of long-lived seabirds (Caswell 2001; Croxall et al. 2012; Phillips et al. 2016). Young or old individuals may be disproportionally impacted by poor environmental conditions because of lower foraging efficiency or differences in distribution, and such changes are likely to become more prevalent under predicted scenarios of global warming (Sydeman et al. 1991). Marine protection measures could benefit some age and sex classes more than others, and potentially target young and mid-aged individuals that will make the most contribution to population growth rate over the long term (Moreno 2003).

CHAPTER 6 – Movements and diving behaviour of white-chinned petrels: diurnal variation and implications for bycatch mitigation

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Author contributions:

I conceived the project, developed the research questions, conducted the data analysis and wrote up the chapter with supervision from R. A. Phillips & A. Manica.

J. Navarro provided coding support with processing the dive data within diveMove in R (see section 6. 2. 2) and provided feedback on all versions of the manuscript.

ABSTRACT

1. Many seabirds dive to forage, and the ability to use this hunting technique varies according to such factors as morphology, physiology, prey availability and ambient light levels. Proficient divers are better able to seize sinking baits deployed by longline fishing vessels and may return them to the surface, increasing exposure of other species. Hence, diving ability has major implications for mitigating incidental mortality (bycatch) in fisheries.

2. Here, the diving behaviour and activity patterns of the most bycaught seabird species worldwide, the white-chinned petrel (*Procellaria aequinoctialis*), tracked from Bird Island (South Georgia), are analysed. Three data sources (dives, spatial movements and immersion events) are combined to examine diverse aspects of at-sea foraging behaviour, and their implications for alternative approaches to bycatch mitigation are considered.

3. The tracked white-chinned petrels (n=14) mostly performed shallow dives (< 3 m deep) of very short duration (< 5 s), predominantly during darkness, but only 7% and 10% of landings in daylight and darkness, respectively, involved diving, suggesting that surface-seizing is the preferred foraging technique. Nonetheless, individuals were able to dive to considerable depth (max = 14.5 m) and at speed (max = 2.0 $m.s^{-1}$), underlining the importance of using heavy line-weighting to maximize hook sink rates, and bird-scaring lines (Tori lines) that extend for long distances behind vessels to protect hooks until beyond diving depths.

6. 1 Introduction

Seabirds vary widely in the manner in which they exploit marine food resources, with diving providing a means of accessing prey at various depths in the water column (Shealer 2002; Elliott et al. 2008). Knowledge of the diving ability of seabirds was revolutionized by the development of electronic time-depth recorders (TDRs) in the 1970s, which use pressure sensors (Kooyman & Campbell 1971). Physiological and anatomical adaptions to pressure, cold temperatures, low light levels and breath-holding determine the maximum dive capabilities (in terms of depth and duration) of different species (reviewed in Ponganis 2015). However, diving is energetically expensive in seabirds, and in practice the frequency and characteristics of dives can differ considerably within and among species according to local prey availability and distribution, ambient light conditions, individual energetic requirements or the degree of inter- and intra-specific competition for food (Croll et al., 1992; Navarro, Votier & Phillips, 2014; Peery et al., 2009; Quillfeldt et al., 2011; Regular et al., 2010).

Determining the extent of diving behaviour and ability across taxa has major conservation implications, as diving can increase the exposure of seabirds to anthropogenic threats (Waggitt & Scott, 2014; Tavares et al., 2017; Zhou, Jiao & Browder, 2019). In particular, incidental mortality (bycatch) of seabirds in longline fisheries has severely depleted the population sizes of many species, especially wide-ranging and long-lived albatrosses and petrels (Anderson et al. 2011; Phillips et al. 2016). These birds forage behind fishing vessels, attracted by discards (including offal) and baited hooks available during the deployment of longlines. Bycatch occurs when birds seize baits, are hooked and drown as the line sinks; proficient divers are most vulnerable as they are able to access baits at greater depths than surface-feeding species (Brothers, 1991; Rollinson, Dilley & Ryan, 2014; Rollinson et al., 2016). As a result, efforts to reduce bycatch in longline fisheries have focused on modifying gear configuration (e.g. required weight and spacing) to increase the rate at which lines sink,

and use of bird-scaring (streamer or Tori) lines to protect baited hooks from attack while they are within seabird diving depths (Løkkeborg, 2011; Melvin, Guy & Read, 2014; Jiménez, Forselledo & Domingo, 2019b). Knowledge of diving range and speed is therefore integral to effective mitigation, which, in turn, is key to the recovery of threatened seabird populations and ecosystem-based management of longline fisheries (Ryan & Watkins, 2002; Sánchez & Belda, 2003; Croxall & Nicol, 2004).

Diving ability among procellariform seabirds varies from minimal submersion to deep dives recorded in more specialized species (Prince, Huin & Weimerskirch, 1994; Weimerskirch & Sagar, 1996; Navarro, Votier & Phillips, 2014). Opportunistic *Procellaria* petrels both surface-seize and dive for prey down to 16m depth; however, it remains unclear whether the latter hunting technique plays a dominant role in their foraging ecology (Huin, 1994; Barnes, Ryan & Boix-Hinzen, 1997; Freeman et al., 1997; Rollinson et al., 2016). In line with optimal foraging theory, animals are expected to favour strategies that maximize net energy gain, thus petrels may increase diving effort (rate, depth or duration) if this improves foraging success (Schoener 1971). The population of white-chinned petrels (*Procellaria aequinoctialis*) breeding at South Georgia is globally-important in terms of population size, and competes with a large diversity of sympatric seabirds for resources (Phillips et al. 2008). To co-exist, niche theory stipulates these species should segregate in spatial, temporal or trophic axes (Hutchinson 1957; Schoener 1974). White-chinned petrels are known to forage to a greater extent over the productive Patagonian Shelf than other seabirds from South Georgia, particularly during the incubation stage (Phillips et al. 2006). Diving may add an additional mechanism resulting in niche partitioning from albatrosses (Diomedeidae) and giant petrels *Macronectes* spp. and, combined with their foraging habitat specialization, may help drive the exceptionally high abundance of white-chinned petrels at South Georgia.

Diving ability is also of relevance in the context of fisheries interactions, as white-chinned petrels are the most bycaught seabird in the Southern Ocean (Phillips et al. 2016).

In this study, high-resolution dive data (0.5 s sampling interval) were analysed, in combination with movement and immersion data, from incubating white-chinned petrels tracked from South Georgia during the 2009/10 breeding season. The aims were to: (1) build a detailed picture of the at-sea foraging behaviour of white-chinned petrels during an energetically-expensive period of their annual cycle, and (2) consider the implications for the design and performance of seabird bycatch mitigation measures in longline fisheries. Specifically, the distribution of foraging trips and diving events were mapped to gain an understanding of exposure to fishing vessels, and metrics of foraging behaviour (landing and diving events) were compared between daylight and darkness. In addition, diving descent rates were calculated for comparison with measured and recommended line sink rates for pelagic and demersal longline fishing vessels operating in the Southern Ocean.

6. 2 Methods

6. 2. 1 Study area and fieldwork procedure

Fieldwork was conducted on subantarctic Bird Island (54°00'S, 38°03'W), South Georgia, which lies 300 km south of the Antarctic Polar Front in the south-west Atlantic Ocean (Figure 6. 1). Due to high productivity around South Georgia and the Antarctic Peninsula, this island hosts millions of pairs of breeding seabirds in one of the world's densest aggregations (Croxall & Prince, 1980; Atkinson et al., 2001; Clarke et al., 2012). It is a globally important breeding site for many species, including white-chinned petrels, which have been steadily declining in population size since the 1970s due to fisheries bycatch (Martin et al. 2009). Fishing effort is restricted around South Georgia during their austral breeding season (CCAMLR 2016), but white-chinned petrels forage almost exclusively over the Patagonian Shelf when incubating; where multiple pelagic and demersal fleets have reported high seabird bycatch rates (Phillips

et al. 2006; Jiménez et al. 2010; Favero et al. 2013). Illegal, unreported and unregulated fishing activities may also be high, and these vessels are highly unlikely to use bycatch mitigation (Agnew et al. 2009).

Sixteen incubating adult white-chinned petrels were tracked from Bird Island during the 2009/10 breeding season (3 December 2009 – 16 January 2010). Birds were fitted with Mk19 geolocator-immersion logger (2.6g; British Antarctic Survey, Cambridge) attached by cable ties to a plastic leg ring, and a G5 time-depth recorder (TDR; 6.5 g, 12 x 36.5 mm; Cefas Technology Ltd) attached with Tesa® tape to the base of 2-3 tail rectrices. Mean body mass ± standard deviation of tracked white-chinned petrels was 1364 ± 100g, and the total mass of devices (geolocators and TDRs) including attachments was therefore far below the 3% threshold of body mass beyond which deleterious effects are more common in oceanic seabirds (Phillips, Xavier & Croxall, 2003). Birds were of unknown sex.

6. 2. 2 Tracking data processing

Geolocators were retrieved from 15 of the 16 instrumented birds in December 2009-January 2010. Locations during foraging trips were estimated from the raw light intensities recorded by the geolocator-immersion loggers according to Merkel et al. (2016). Twilight events were first estimated using the function 'preprocessLight' function in the 'TwGeos' package, with a threshold setting of 2 lux, an offset of 12 hours and a maximum light level of 74,418.6 lux. Locations were then computed from the twilight events using the 'prob_algorithm' function in the 'probGLS' package. This function uses an iterative, forward-step-selection, probabilistic algorithm that incorporates information on various sources of uncertainty, the behaviour of the study species, and the characteristics of the environment to generate the most likely movement path (Table S5. 1). Two locations, corresponding to local midday and midnight, were generated per day with a median error of up to 185 km (Merkel et al. 2016). Resulting points were removed if they required unrealistic flight speeds (>35 km.h-1

sustained over a 48 h period; Phillips et al. 2004b), or for the bird to cross over land. The loggers also tested for saltwater immersion every 3 s, recording the time of transitions between wet/dry states that lasted ≥ 6 s, providing the timing and duration of flights and landings. White-chinned petrels are burrow-nesting birds, and depart and return to their burrows during darkness, making it difficult to accurately estimate the start and end times of foraging trips. Therefore, foraging trips were trimmed to the first and last-recorded immersion event.

TDRs were retrieved from 14 of the 15 birds recaptured in 2009/10 (one had moulted its tail feathers). TDRs were programmed to record pressure continuously at a low sampling interval (three and five second intervals; see Table S5. 2 for full sampling regime) every day (4 birds) or every third day (10 birds). A fast-logging mode was also set to record pressure at a high sampling interval (0.5 seconds), activated by entry into water. A comparison of the dives identified post-processing (detailed below) indicated there was little difference between the recording modes in terms of the number and timing of dive events (Table S5. 3). A higher number of dives were identified from the continuous dive recording datasets; however, these dives mostly consisted of a single data point (and were likely noise), and the fast-logging mode detected short dives missed by the coarser sampling regime (Table S5. 3). Therefore, in order to standardize the comparison of diving behaviour across all tracked birds, only the fast-logging data were used for subsequent analyses. Continuous time-series were generated from these data by manually setting depth to 0 m in between the dives (Figure S5. 1). Zero offset correction was then carried out using the function ‘calibrateDepth’ in the package ‘diveMove’ (Luque & Fried, 2011). ‘calibrateDepth’ uses recursive filtering and a diving threshold to correct for noise and drift in the depth sensor, and to identify diving behaviour. Dive threshold was set at 1m depth, and dives that lasted < 1 s, or were very deep (>10m)

with few data points (< 5) were considered to be noise or recording errors and hence removed, resulting in a total sample size of 895 dives from 14 individual birds.

6. 2. 3 Analysis of immersion and dive data

Approximate dive locations were estimated by interpolating the twice-daily geolocator positions, and the core (50%) and general (90%) kernel density distributions of dives generated using the R package 'adehabitatHR' (Calenge 2006). A grid size of 5 km and a smoothing parameter of 185 km were chosen to account for geolocation error (Merkel et al. 2016). Kernel distributions of dive events were overlaid on the extent of Exclusive Economic Zones (Flanders Marine Institute 2014), and Statistical Areas, Subareas and Divisions used by the Convention for the Conservation of Antarctic Marine Living Resources (CCAMLR; https://data.ccamlr.org/dataset/statistical-areas-subareas-and-divisions [Accessed 27th February 2020]). The kernels were also overlaid on the main areas of operation during December and January of demersal longline vessels from Argentina and the Falklands Islands from 1997 to 2007, which were the most recent publicly available data by month (Tuck et al. 2016), and of pelagic longline vessels operating under the jurisdiction of the International Commission for the Conservation of Atlantic Tunas (ICCAT) from 2000 to 2010 (Task II catch/effort; https://www.iccat.int/en/accesingdb.html [Accessed 27th February 2020]).

In order to investigate the effects of ambient light levels on at-sea activity (including diving) patterns, immersion (wet) events and dives were assigned to daylight or darkness according to the timing of twilight using the 'TwGeos' package. The following mean activity metrics were calculated separately for the daylight and darkness periods of each foraging trip; (1) proportion of time spent wet; (2) landing rate (wet events, i.e. wet-dry transitions, per hour); (3) wet bout length (minutes); (4) dry bout length (minutes); (5) dive duration (minutes, calculated using function 'divestats'); (6) dive depth (metres, calculated using function

'divestats'); (7) maximum descent rate ($m.s^{-1}$, calculated as the maximum of speeds travelled by a bird between every consecutive point during the descent phase); (8) dive rate ($dives.hr^{-1}$); and (9) proportion of landings that were dives. One bird completed three foraging trips, but only dived during one of these, and metrics were calculated for this trip only (TRACKID: 19013_3, Table 6. 1). The normality of metrics (1-9) were investigated using the Shapiro-Wilk test, and parametric paired *t*-tests or non-parametric Wilcoxon signed-rank tests were used, as appropriate, to compare metrics between daylight and darkness.

Finally, every dive was assigned to a maximum depth band (one metre depth intervals; 1-2m, 2-3m etc.), and average descent rates (i.e. diving speeds) of white-chinned petrels over a range of depth bands were compared with longline sink rates measured at sea on pelagic and demersal vessels operating in the Southern Ocean (see Table S5. 4 for references).

All data analyses were conducted with the software R 3.6.2. (R Core Team 2020). In results, means ± standard deviations (SD) are presented, unless indicated otherwise.

6. 3 Results

6. 3. 1 Overall foraging distribution and diving behaviour

Incubating white-chinned petrels tracked during the 2009/10 breeding season from Bird Island foraged over a large area mainly west and north west of Bird Island on trips that lasted 3.6-19.3 days (Figure 6. 1a, Table 6. 1). Most birds travelled directly west to the Patagonian Shelf (between 45-25°S), where most diving events occurred (Figure 6. 1b). A smaller number of birds travelled to the north and north east of South Georgia, and two to the south west (~ 50°S) (Figure 6. 1a), resulting in four, more restricted diving hotspots over oceanic waters, around the Antarctic Polar Front, and south east of the Falklands (Figure 6. 1b). The core diving area (50% kernel polygon) on the Patagonian Shelf occurred largely within the

EEZs of Argentina and the Falkland Islands, and overlapped extensively with demersal longline effort in December and January (Figure 6. 2b). The northern portion of this area also overlapped with pelagic longline fleets operating within the jurisdiction of ICCAT (Figure 6. 2c). All diving hotspots occurred outside of CCAMLR subarea 48.3, where demersal longline fishing is prohibited during summer months, when white-chinned petrels are breeding (Figure 6. 2a; CCAMLR 2016).

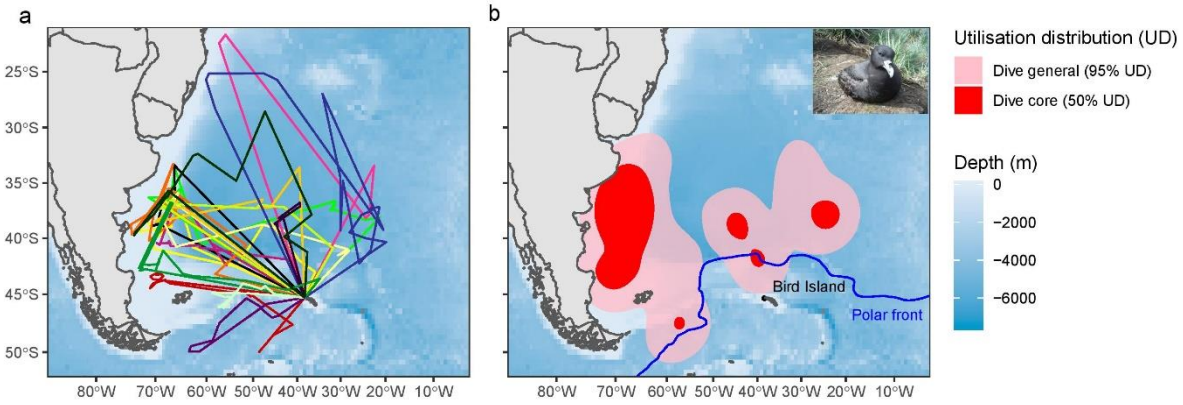

Figure 6. 1: (a) Foraging trips of 15 incubating white-chinned petrels tracked from Bird Island (South Georgia) during the 2009/10 breeding season using geolocators. Locations were estimated using the 'ProbGLS' package, and individual foraging trips are represented by different colours. (b) Core (50%) and general (95%) utilisation distributions of diving events.

Table 6. 1: Dive characteristics of white-chinned petrels tracked from Bird Island (South Georgia) tracked during the incubation period in the 2009/10 breeding season. N days dive data = number of days within the foraging trip with dive data. N days dive = number of days within the foraging trip during which dives took place.

Ring	Trip	Start trip[a]	End trip[b]	Duration (days)	N days dive data : N days dives	Dives per day		Dive duration (s)			Dive depth (m)			Descent rate ($m.s^{-1}$)[c]		
						Max	Mean ± SD	Max		Mean ± SD	Max		Mean ± SD	Max		Mean ± SD
								Daylight	Darkness		Daylight	Darkness		Daylight	Darkness	
HT65341	1	2009-12-05	2009-12-20	15.1	5: 2	10	8.50 ± 2.12	9.50	14.0	5.38 ± 3.67	4.87	6.87	3.32 ± 1.45	1.50	1.50	0.81 ± 0.53
HT65342	1	2009-12-11	2009-12-25	14.8	5: 4	61	20.8 ± 27.1	14.0	16.0	5.26 ± 3.59	6.75	8.50	3.71 ± 1.78	1.56	1.68	0.94 ± 0.46
HT65343	1	2009-12-07	2009-12-18	11.5	4: 4	4	2.50 ± 1.73	23.5	8.00	9.05 ± 7.40	12.2	3.03	5.05 ± 3.90	1.56	0.88	0.88 ± 0.47
HT65344	1	2009-12-07	2009-12-10	3.55	1:0	-	-	-	-	-	-	-	-	-	-	-
HT65344	2	2009-12-13	2009-12-22	9.44	3:0	-	-	-	-	-	-	-	-	-	-	-
HT65344	3	2009-12-24	2009-12-29	5.66	2: 1	12	-	20.5	5.00	6.25 ± 5.94	4.21	4.00	3.11 ± 0.87	1.26	1.32	0.80 ± 0.46
HT65345	1	2009-12-07	2009-12-19	12.8	4: 2	10	7.50 ± 3.54	30.5	23.0	10.6 ± 8.37	8.28	4.09	4.22 ± 1.93	1.50	0.82	1.02 ± 0.34
HT65346	1	2009-12-19	2009-12-25	6.19	2: 2	96	80.5 ± 21.9	19.0	12.5	3.69 ± 2.64	7.81	5.03	2.23 ± 0.77	1.56	1.26	0.46 ± 0.37
HT65347	1	2009-12-17	2009-12-27	10.3	4: 2	11	7.00 ± 5.66	2.50	-	1.64 ± 0.66	2.78	-	1.94 ± 0.40	0.32	-	0.21 ± 0.08
HT65348	1	2009-12-06	2009-12-19	13.7	5: 4	19	9.00 ± 8.04	17.5	13.5	3.07 ± 3.68	6.90	6.68	2.54 ± 1.46	1.32	1.32	0.59 ± 0.57
HT65350	1	2009-12-06	2009-12-18	12.7	5: 3	16	12.7 ± 3.51	13.0	10.5	5.05 ± 3.43	6.68	4.18	3.21 ± 1.29	1.62	1.38	1.00 ± 0.43
MA13701	1	2009-12-18	2010-01-01	14.4	4: 4	25	14.8 ± 10.1	22.0	3.50	3.58 ± 4.20	14.5	3.06	3.01 ± 2.32	1.82	1.20	0.85 ± 0.48
MA13702	1	2010-01-01	2010-01-14	13.3	14: 10	38	14.5 ± 10.7	18.0	23.0	5.03 ± 3.82	8.62	11.4	2.85 ± 1.48	2.00	1.56	0.75 ± 0.53
MA13703	1	2009-12-26	2010-01-10	15.5	16: 9	8	4.11 ± 3.10	20.0	12.0	6.64 ± 5.29	7.78	5.96	3.33 ± 1.72	1.62	1.56	0.87 ± 0.43
MA13704	1	2009-12-24	2010-01-12	19.3	19: 13	82	17.3 ± 27.9	12.5	16.0	4.81 ± 3.35	7.06	6.00	2.44 ± 1.09	1.56	1.50	0.68 ± 0.42
MA13705	1	2009-12-28	2010-01-08	11.8	12: 7	29	6.14 ± 10.2	7.50	13.5	4.33 ± 2.85	3.18	3.37	2.11 ± 0.46	0.94	0.64	0.32 ± 0.21
MA13706	1	2010-01-03	2010-01-14	11.7	TDR lost											

[a]Start of trip corresponds to the first immersion event

[b]End of trip here corresponds to the last immersion event

[c]Values exclude all negative descent rates (i. e. when the bird ascended slightly during the descent phase of a dive).

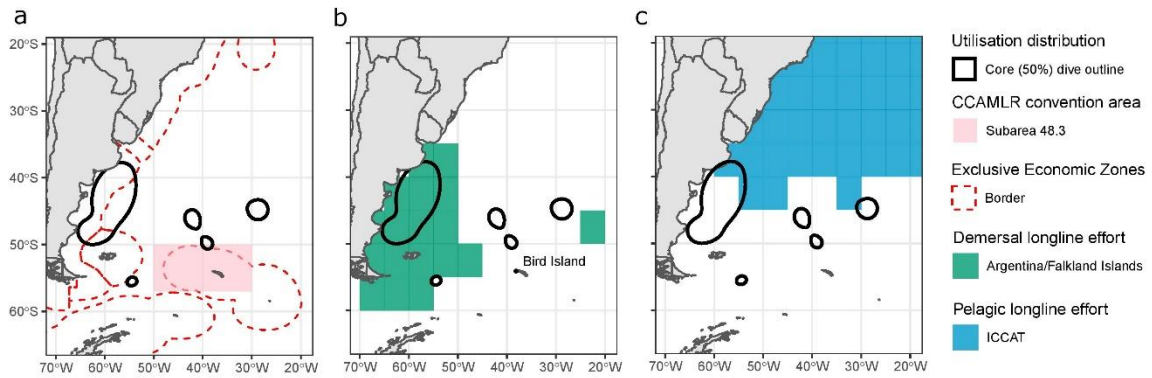

Figure 6. 2: Core (50%) utilization distribution of diving events from incubating white-chinned petrels tracked from Bird Island (South Georgia) during the 2009/10 breeding season in relation to (a) Exclusive Economic Zones and Convention for the Conservation of Antarctic Marine Living Resources (CCAMLR) convention subarea 48.3, (b) mean 5x5° grid cell distribution of demersal longline fishing for Argentina and the Falkland Islands (averaged for December-January over 1997-2007), and (c) mean 5x5° grid cell distribution of pelagic longline fishing of fleets operating under the jurisdiction of the International Commission for the Conservation of Atlantic Tunas (ICCAT) (averaged for December-January over 2000-2010).

Diving behaviour varied considerably among individuals in terms of number of dives per day (range: 0-96), duration (1-30.5 seconds), maximum depth (1.03-14.46 m) and maximum descent rates (0.06-2.00 $m.s^{-1}$), however, on average individuals made few (< 10 $dives \cdot day^{-1}$), shallow (< 3m depth) and short dives (< 5 s; Table 6. 1 and Figure 6. 3).

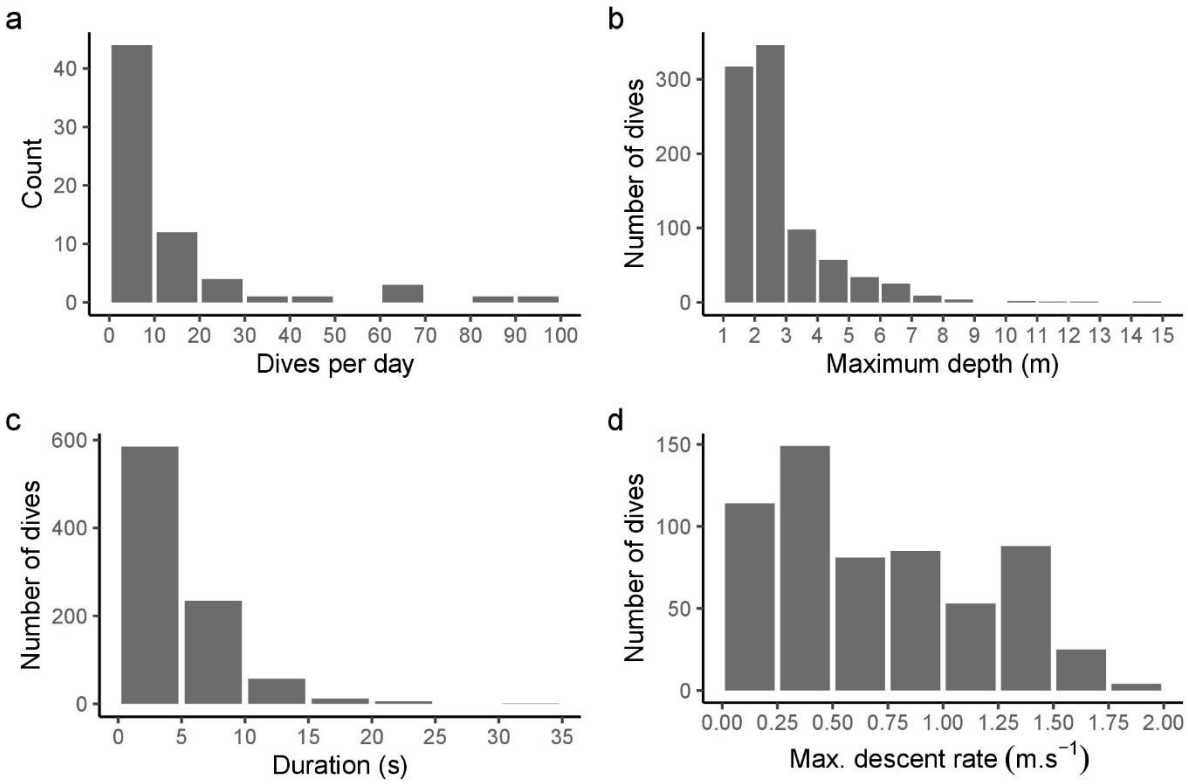

Figure 6. 3: Frequency distributions of dive metrics of 14 incubating white-chinned petrels tracked from Bird Island (South Georgia) during the 2009/10 breeding season; (a) total dives per day, (b) maximum dive depths, (c) dive durations, and (d) maximum dive descent rates.

6. 3. 2 Diurnal variation in immersion and dive metrics

Table 6. 2: Comparison of dive and other activity (immersion) metrics between daylight and darkness of white-chinned petrels tracked from Bird Island (South Georgia) during the 2009/10 breeding season. Paired t-tests or Wilcoxon signed-rank tests used for normal or non-normal data, respectively. Significant differences (p<0.05) are highlighted in bold.

Metric	Sample size	Sample mean ± standard deviation		Paired t-test/Wilcoxon signed-ranks test
		Daylight	Darkness	
(1) Proportion wet	15	0.30 ± 0.10	0.36 ± 0.93	**t_{14} = -3.310, p = 0.005**
(2) Landing rate (landings.hr^{-1})	15	2.35 ± 1.07	3.68 ± 1.04	**t_{14} = -2.337, p = 0.013**
(3) Length wet bouts (mins)	15	9.01 ± 4.65	6.06 ± 1.98	**V = 100, p = 0.022**
(4) Length dry bouts (mins)	15	19.1 ± 7.00	10.1 ± 4.55	**V = 107, p = 0.005**
(5) Dive depth (m)	13[a]	3.57 ± 1.18	2.65 ± 0.58	**V = 78, p = 0.021**
(6) Dive duration (s)	13[a]	6.31 ± 2.94	4.60 ± 1.60	V = 115, p = 0.124
(7) Max descent rate (m.s^{-1})	13[a]	0.89 ± 0.19	0.67 ± 0.25	**t_{12} = 2.756, p = 0.017**
(8) Dive rate (dives.hr^{-1})	13[a]	0.14 ± 0.18	0.42 ± 0.54	**V = 11, p = 0.013**
(9) Proportion landings that were dives	13[a]	0.07 ± 0.05	0.10 ± 0.09	V = 37, p = 0.0588

[a] One Time-Depth Recorder was not recovered, and one bird did not dive during darkness.

There was strong evidence for diurnal variation in the diving behaviour and other at-sea activities of tracked white-chinned petrels. Birds were more active during darkness than daylight; they spent a significantly higher proportion of time wet (Figure 6. 4a and Table 6. 2), landed more often on the water (Figure 6. 4b and Table 6. 2), and landing bouts were of shorter duration (Figure 6. 4c and Table 6. 2). Wet and dry bouts were significantly shorter in duration during darkness than daylight (Figures 6. 4c & d and Table 6. 2), suggesting birds both rested and undertook longer transit flights during the day. Birds also dived significantly more often during darkness than daylight (Figure 6. 5d and Table 6. 2), but those dives were significantly less deep (Figure 6. 5a and Table 6. 2), and descent rates were slower (Figure 6.

5c and Table 6. 2). Dives were also shorter on average during darkness than daylight, but this difference was not significant (Figure 6. 5b and Table 6. 2). Only 7% and 10% of landings during daylight and darkness, respectively, were dives (Figure 6. 5e and Table 6. 2), suggesting that surface-feeding is the dominant foraging strategy regardless of ambient light-levels.

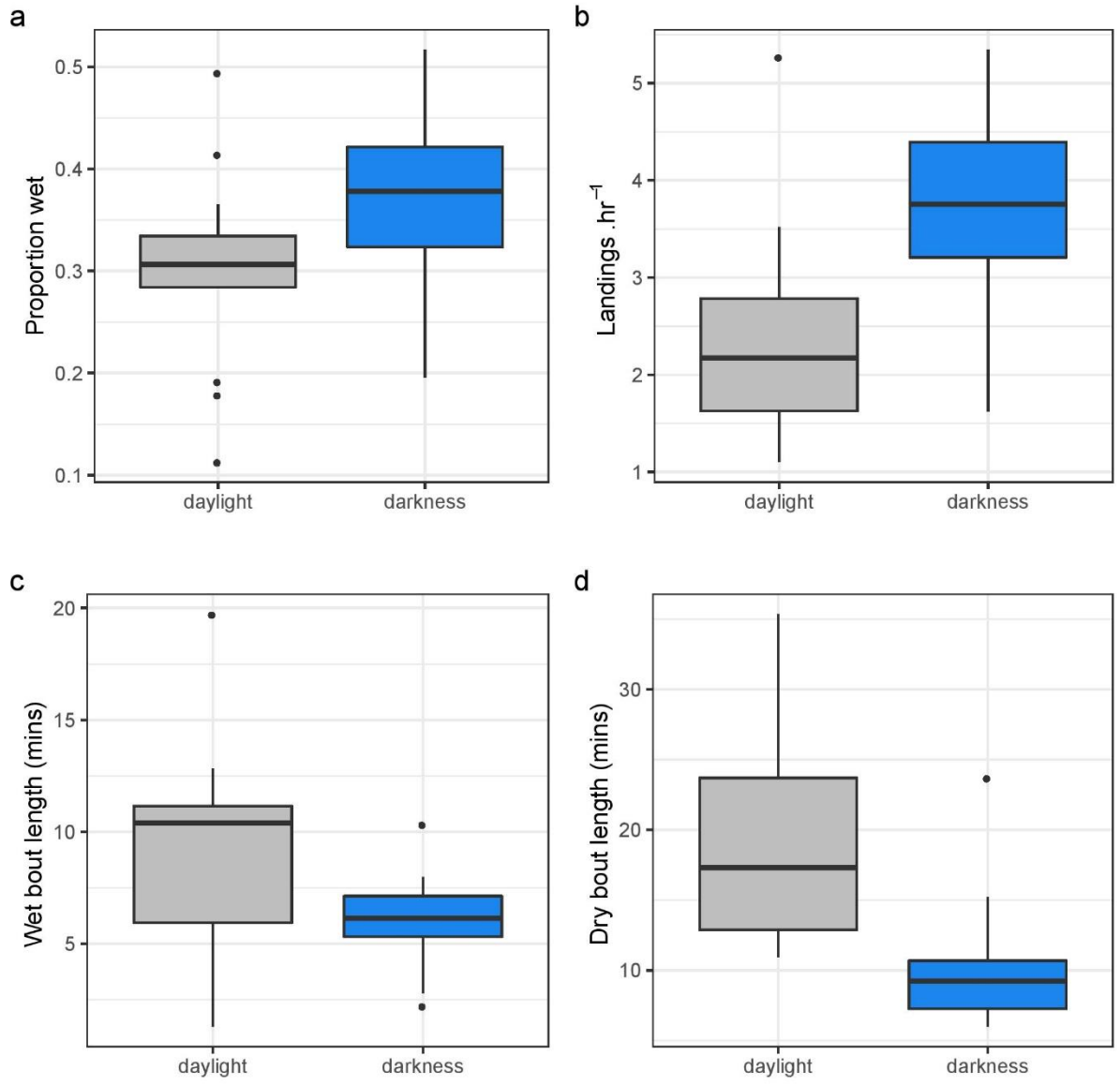

Figure 6. 4: Comparison of activity (immersion) patterns between daylight and darkness of 15 incubating white-chinned petrels tracked from Bird Island (South Georgia) during the 2009/10 breeding season.

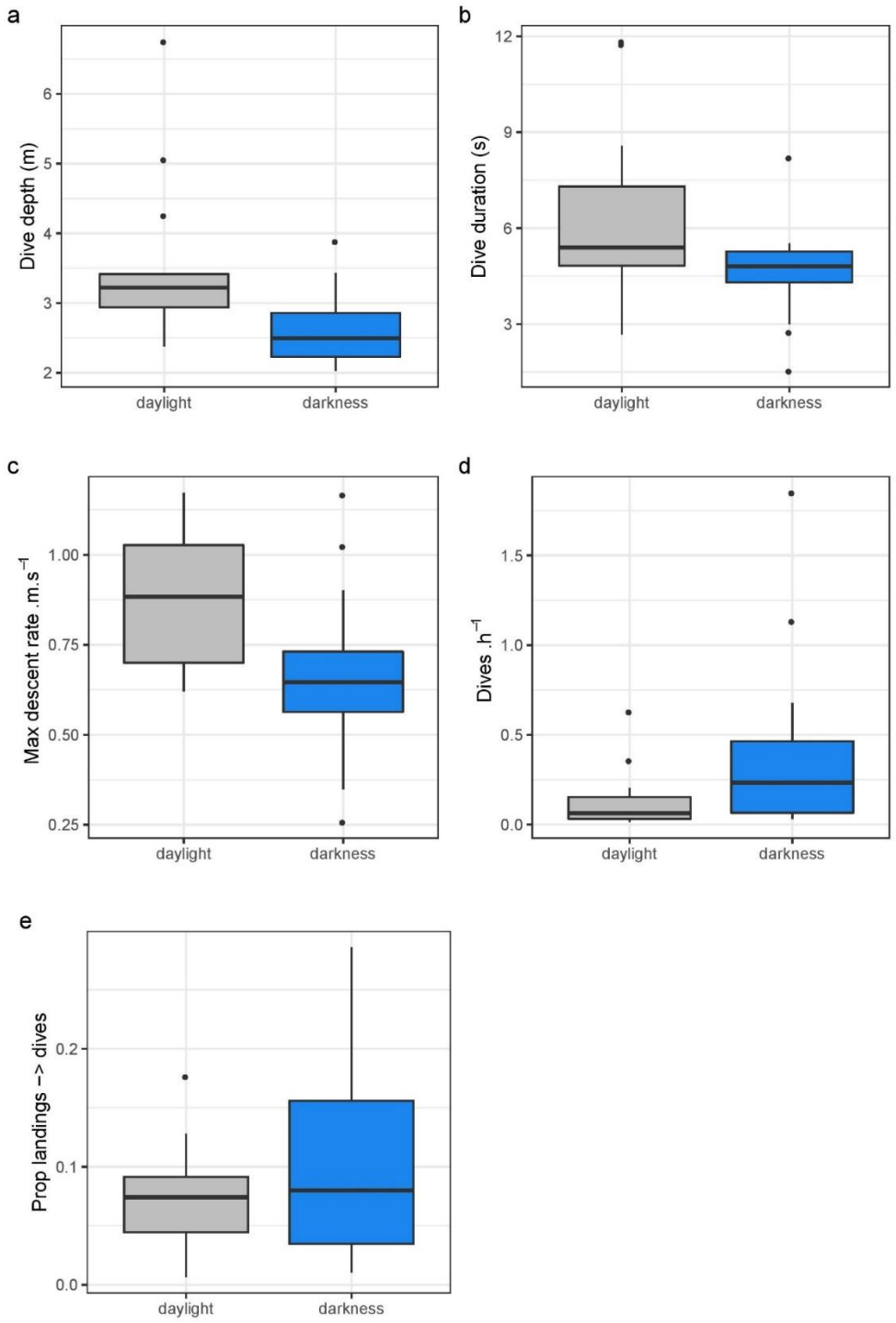

Figure 6. 5: Comparison of dive behaviour of 13 white-chinned petrels between daylight and darkness. Fifteen incubating white-chinned petrels were tracked from Bird Island (South Georgia) during the 2009/10 breeding season, Time-Depth Recorders were retrieved from 14 birds, and one bird did not dive during darkness.

6. 3. 3 Comparison of descent speeds with published longline sink rates

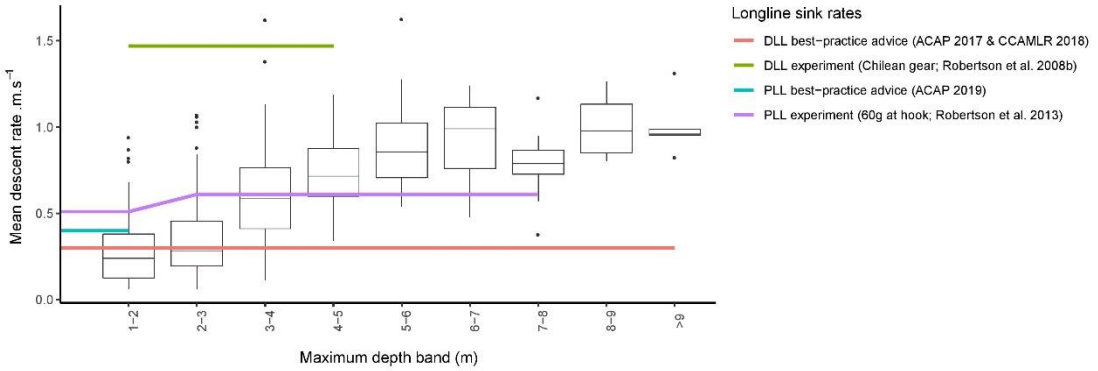

Figure 6. 6: Mean diving descent rates in relation to maximum depth achieved by incubating white-chinned petrels tracked from Bird Island (South Georgia) during the 2009/10 breeding season. Fastest published and advised line sink rates for pelagic (PLL) and demersal (DLL) longline fisheries operating in the Southern Ocean are shown for comparison (see Table S5. 4 for full details). Depth range over which link sink rates extend represent the range over which they were measured, or to which best-practice advice extends.

Mean descent rates of white-chinned petrels increased on average with increasing dive depth (Figure 6. 6), and plateaued around the 5-6m maximum depth band (~ 1.0 $m \cdot s^{-1}$, although one bird descended on average > 1.5 $m \cdot s^{-1}$ during two separate dives). While descent rates were much slower during the shallow dives (median dive descent rate < 0.5 $m \cdot s^{-1}$ for dives up to 3m depth), birds descended at > 0.9 $m \cdot s^{-1}$ during at least one dive in each maximum depth band, suggesting this descent speed can be achieved across all diving depths. This speed exceeds recommended line sink rates for both pelagic and demersal longlines on vessels operating in the Southern Ocean, as well as the fastest sink rate recorded within a pelagic longline fishery sustained over > 3m (0.51-0.61 $m \cdot s^{-1}$ achieved with a 60g safe-lead swivel placed at the hook; see Figure 6. 6 and Table S5. 4 for full gear configuration and

experimental details). The only demersal longline fishery in the Southern Ocean in which a faster sink rate was achieved was in an experiment using the Chilean net-sleeve ('cachalotera') gear configuration, which recorded sink rates of 1.47 $m \cdot s^{-1}$ between 2-5m depth by attaching 6kg steel weights at 40m intervals along longlines; Figure 6. 6 and Table S5. 4).

6. 4 Discussion

By combining individual movement, immersion and TDR data, this study confirms that white-chinned petrels dive at the Patagonian Shelf, and provides new insights into their at-sea activity patterns, particularly the importance of nocturnal feeding. These new findings underline the opportunistic foraging abilities of this threatened seabird, and are discussed in the context of effective design of bycatch mitigation measures.

6. 4. 1 Insights into the foraging ecology of white-chinned petrels

The diving capabilities of white-chinned petrels from South Georgia were comparable to previous studies in terms of maximum depth, duration and descent rate; 14.5 m, 30.5 s and 2 $m.s^{-1}$ (this chapter) *vs.* 12.8-16.1 m, 22 s and 1.58 $m.s^{-1}$ (Huin, 1994; Rollinson, Dilley & Ryan, 2014). White-chinned petrels possess ocular and osteological adaptations to their aquatic lifestyle (Kuroda, 1954; Martin & Prince, 2001), and are more competent divers than southern hemisphere albatrosses, of which the deepest dive recorded (to 12.4 m, based on a capillary-tube depth gauge) was by a light-mantled albatross *Phoebetria palpebrata* (Prince, Huin & Weimerskirch, 1994; Huin & Prince, 1997; Hedd et al., 1997). In terms of dive depth, however, the white-chinned petrel is far surpassed in capability by more specialized procellariform species, including the short-tailed shearwater *Ardenna tenuirostris,* (71 m; Weimerskirch & Cherel, 1998), and also the sympatric South Georgian diving petrel *Pelecanoides georgicus* (18.1 m; Navarro, Votier & Phillips, 2014). Indeed, only a very low proportion (7-10%) of landings by the tracked white-chinned petrels in the study involved

diving, implying that surface-seizing of prey is their primary hunting technique. As diving is energetically-expensive, especially in shallow waters (Wilson et al. 1992), individuals may only pursue prey underwater when conditions are suitable, or to obtain prey that are highly nutritious (Peery et al. 2009; Dean et al. 2013).

Regardless of foraging technique, white-chinned petrels are capable of hunting during daylight and darkness (Harper, 1987; Péron et al., 2010; Mackley et al., 2011; Rollinson, Dilley & Ryan, 2014). Based on the pattern in landings seen here, birds foraged most actively at night. The extent to which this behaviour is targeted at natural prey versus fisheries discards is unknown. White-chinned petrels from South Georgia overlap in distribution with longline fisheries operating along the Patagonian coast during the breeding and non-breeding season, and may specialize in scavenging behind vessels that set their lines at night (Phillips et al., 2006; Robertson et al., 2006; Laich & Favero, 2007; this chapter). However, during chick-rearing, this species predominantly feeds on Antarctic krill (*Euphausia superba*), squid and myctophid fish, of which some species vertically-migrate to shallower depths during darkness (Roper & Young, 1975; Croxall et al., 1985; Croxall et al., 1995; Berrow & Croxall, 1999; Shreeve et al., 2009). These birds may thus be well-adapted to detecting prey under low light levels, and diving at night may allow individuals to spot prey with ventral bioluminescence from below (Imber 1976; Young 1977; Croxall et al. 1995). Deploying stomach temperature loggers would provide additional insight into whether individuals rest on the water during the darkest periods of the night, or whether they continue to feed, potentially using the sit-and-wait method (Wilson et al., 1995; Weimerskirch, Wilson & Lys, 1997; Catry et al., 2004).

In contrast, bouts of flying or sitting on the water were of significantly longer duration during daylight. As these birds are proficient nocturnal hunters, individuals may choose to rest for long periods during daylight, and avoid competing with large aggregations of diurnal

albatrosses and petrels with which they overlap in distribution (e. g. sooty shearwaters, *Puffinus griseus*, or black-browed albatrosses, *Thalassarche melanophris*, from the Faklands Islands Huin 2002; Hedd et al. 2014). White-chinned petrels transit rapidly, taking just 1-2 days to move between the colony at South Georgia and their main prey-rich foraging grounds at the Patagonian Shelf, which may account for the long flight bouts. It is unclear why these transit flights would be restricted to daylight however, as previous research concluded that these birds were just as proficient at flying during darkness (Berrow, Wood & Prince, 2000b; Mackley et al., 2011). As individual flight bouts were on average much shorter than in non-breeding white-chinned petrels commuting to their wintering areas (~ 19 vs 107 minutes), it is possible that the long daylight flights indicate an alternative foraging strategy involving prey searching over larger spatial scales than in darkness (Weimerskirch, Wilson & Lys, 1997; Mackley et al., 2011). This difference would presumably reflect some limitation in their ability to detect more distant prey from the air when light levels are low, which was suggested as the main factor limiting nocturnal foraging of albatrosses (Phalan et al. 2007).

6. 4. 2 Relevance of diving behaviour for the design of bycatch mitigation measures

Demersal longline fishing for Patagonian toothfish (*Dissostichus eleginoides*) historically resulted in high rates of white-chinned petrel bycatch near the colonies at South Georgia (Dalziell & Poorter, 1993). However, seasonal closure of this fishery (in CCAMLR Subarea 48.3; see Figure 6. 2) alongside the implementation of several mitigation measures; prohibition or limiting of offal discharge, use of bird-scaring devices, night-setting and heavy line-weighting, has drastically reduced bycatch of seabirds, including white-chinned petrels (Croxall 2008). Birds from the South Georgia population, however, commute to the Patagonian shelf to forage during incubation, where they overlap in distribution with other longline fisheries for which there is recorded bycatch; namely demersal vessels from the Falklands targeting Patagonian toothfish, and to a lesser extent vessels from Argentina which

also target pink cusk-eel *Genypterus blacodes*, and yellow-nose skate *Dipturus chilensis*, and pelagic vessels operating under the jurisdiction of ICCAT targeting tuna, swordfish and pelagic sharks (Phillips et al., 2006; Otley, Reid & Pompert, 2007; Bugoni et al., 2008; Jiménez et al., 2010; Favero et al., 2013). The major diving hotspot of white-chinned petrels in the study overlapped with these fishing areas, confirming that individuals are particularly susceptible to bycatch in this region during incubation. The South Georgia population furthermore overwinters in this productive area, where it is generally susceptible to bycatch all year-round, and more so than other Procellariform species (Phillips et al. 2016; Clay et al. 2019; Chapter 2). Therefore, although dive capabilities (maximum depth and descent rates) may vary somewhat among seasons (Rollinson, Dilley & Ryan, 2014), recorded dive characteristics in this study provide a relevant baseline for assessing the design and implementation of effective mitigation measures in the south-west Atlantic.

Although white-chinned petrels are far from the deepest-diving of flying seabirds (see review in Navarro, Votier & Phillips, 2014), their mean descent speeds are comparable to those of other bycaught seabird species in the Southern Ocean, including more proficient divers such as the great shearwater *Ardenna gravis* (> 0.9 m.s-1; Hedd et al. 1997; Ronconi et al. 2010; Quillfeldt et al. 2011; Bell 2016; Rollinson et al. 2016). As this velocity across dives of varying depth exceeds all but one published line sink-rate (Table S5. 4), it is apparent that white-chinned petrels and other species are capable of reaching sinking longline hooks within their diving range, and facilitate secondary catch of poorer divers such as albatrosses by returning those hooks on long leaders (snoods) to the surface (Jiménez et al. 2012). Maximising line sink rates is thus an essential mitigation measure as recommended by the Agreement on the Conservation of Albatrosses and Petrels (ACAP, 2017; ACAP, 2019), which can be achieved in pelagic longline fleets by adding sliding leads (recommended minimum standards: >= 4.m.s-1 using 40, 60 or 80g within 0.5, 1 or 2m of the hook; ACAP,

2019; maximum of 0.51-0.61 m.s-1 achieved by using 60g at the hook; Robertson, Candy & Hall, 2013), and in demersal longline fleets by attaching weights close together on the mainline (recommended minimum standards: >0.3 m.s-1 using 5 kg weights at 40 m intervals; ACAP, 2017; maximum of 0.37-0.44 m.s-1 achieved in autoline system using 6.5 kg weights at 35 m intervals, and maximum of 0.33-0.80 m.s-1 achieved in Spanish system using 8kg steel weights at 40m intervals; Robertson, 2001; Robertson et al., 2008). Alternatively, the Chilean net-sleeve demersal longline system, developed to reduce depredation by killer (*Orcinus orca)* and sperm (*Physeter microcephalus)* whales, has virtually eliminated seabird bycatch as baited hooks are directly above weights, ensuring a very high initial line sink rate (up to 1.47 m.s-1; Moreno et al., 2006, Moreno et al., 2008; Robertson et al., 2008). This gear design has since been used by vessels targeting toothfish in the Falklands, but more research is needed to maximize catch per unit effort, reduce fish bycatch and scavenging of catch to facilitate its wider implementation (Brown et al. 2010).

To further reduce the impact of longline fisheries on seabirds, ACAP recommends combining appropriate weighting regimes with the use of other best practice mitigation measures; bird-scaring lines and night-setting (ACAP, 2017; ACAP, 2019). Bird-scaring lines are designed to protect baits while they sink; recognized best practice is to deploy one or two lines which reach an aerial extent of >75 or >100 m in small (< 24 and < 35 m for demersal and pelagic longline vessels, respectively) and large vessels (≥ 24 m and ≥ 35 m for demersal and pelagic longline vessels, respectively), respectively (ACAP, 2017; ACAP, 2019). It is, however, essential that baits are protected until they sink beyond diving range of white-chinned petrels (c. 15m depth); requiring the simultaneous use of a suitable weighting regime. For instance, a large demersal longline vessel setting lines at a speed of 5.5-6.5 knots and using 6.5kg weights spaced at 35m intervals with a bird-scaring line providing 100 m of aerial coverage would protect baits until they reach 12m depth, while a large pelagic longline vessel may

protect baits until 15m depth by setting lines at 9.8 knots using a double-weighted branchline (65-70g) at 2 m from the hooks with a bird-scaring line providing 100 m of aerial coverage (Robertson, 2001; Melvin, Guy & Read, 2014). Baits can similarly be protected by releasing hooks at depth using underwater setting (funnel, chute, and capsule) or hook-shielding devices (hookpod) (Ryan & Watkins, 2002; Gilman, Boggs & Brothers, 2003; Robertson et al., 2018; Sullivan et al., 2018; Jiménez et al. 2020). My results underline the importance of attaining a target release depth of c. 15m. Finally, although night-setting is unlikely to deter white-chinned petrels given the degree of nocturnality and ability to dive deep during darkness (11.5 m) indicated in my study, this mitigation method substantially reduces bycatch of diurnal seabirds, and potentially even of nocturnal species under low light conditions if bird-scaring lines protect sinking baits until they are no longer visually detectable (Jiménez 2020) .Lines should be set between the end of nautical twilight and before nautical dawn (ACAP, 2017; ACAP, 2019) and where possible with minimal deck lighting (Weimerskirch, Capdeville & Duhamel, 2000; Bull, 2007; Jiménez et al., 2019a).

6. 4. 3 Conclusions

White-chinned petrels from South Georgia tracked during the incubation period predominantly landed on the water to forage during darkness, but all birds also fed in daylight indicating a high degree of flexibility. This array of foraging abilities clearly gives this petrel a competitive advantage over other medium to large flying seabirds feeding within its distribution, given the size of the breeding population at South Georgia (1 million breeding pairs; Martin et al. 2009). Conversely, these traits render this bird particularly vulnerable to bycatch in longline fisheries, which can only be avoided by effective mitigation measures (in particular heavy line-weighting and bird-scaring lines). This requires monitoring of implementation and bycatch rates, and enforced compliance (Phillips et al. 2016).

CHAPTER 7 – General discussion

Determining the processes influencing capacity and motivation for movement constitutes a primary goal for ecologists and is of high conservation value given the consequences for individual fitness and population dynamics. Oceanic seabirds offer an ideal study system for such investigations as they are some of the most mobile species on Earth and their movements are relatively easy to record using tracking devices. This group of birds is also highly threatened and tracking studies provide an important diagnostic tool for assessing exposure of individuals to diverse threats in the marine environment. Here, I use tracking data collected from several species of albatrosses and large petrels breeding at Bird Island, South Georgia (54°00'S, 38°03'W), to fill key knowledge gaps in their at-sea distribution and behaviour and assess the consequences in terms of susceptibility to bycatch in fisheries; the biggest threat to the survival of oceanic seabirds.

In early life, I show that external cues and in particular, prevailing winds, play an important role in driving the initial movements of naïve individuals (Chapters 2 and 3). In contrast, adults typically follow more direct routes to known foraging grounds, resulting in age-specific distributions and potential bycatch risk. I use these insights to highlight new areas and fleets of conservation concern that are specific to immature age classes (Chapters 2 and 4). I show that their movement strategies are not fixed even after birds recruit into the breeding population, but can vary according to a complex interaction between sex, breeding status and age (Chapter 5). Building a detailed picture of at-sea behaviour is important for understanding population dynamics, and I demonstrate that this information can be used to assess alternative management strategies, such as the effectiveness of different fisheries-bycatch-mitigation measures, including those considered to be best practice (Chapter 6). In this general discussion, I consider how my findings provide new insights into the extrinsic

and intrinsic processes responsible for shaping movements over the lifespans of individuals, and summarize the implications for conservation. I finish by suggesting avenues for future research made possible by new and exciting advances in tracking technology, and of high priority given anticipated future environmental change.

7. 1 Spatial ecology: insights into the drivers of seabird movement patterns

7. 1. 1 Early life: factors shaping dispersal and development of movement strategies

Environments are heterogeneous and this is particularly true of the dynamic ocean, yet oceanic seabirds are expected to optimize the acquisition of resources in ways that maximize their fitness (Schoener 1971; Baird 1991; Fauchald 1999). Some of the variation among adults in foraging behavior relates to sex, age, breeding status etc., but birds also show some degree of individual preference in terms of foraging destinations, migratory behavior and diets (Patrick & Weimerskirch 2014; Delord et al. 2019; Zango et al. 2019). It remains unclear, however, as to how these different strategies develop (Hazen et al. 2012). By characterizing the movements of juvenile white-chinned petrels (*Procellaria aequinoctialis*) and grey-headed albatrosses (*Thalassarche chrysostoma*) from South Georgia for the first time, I provide new insights into the environmental mechanisms involved in wide-ranging and very long-lived species.

According to the movement ecology paradigm, obtaining and processing external information is key to deciding when and where to move in many organisms. In Chapters 2 and 3, I demonstrate this is especially true of naïve individuals (Nathan 2008). Juvenile white-chinned petrels and grey-headed albatrosses dispersed away from their natal colonies along routes that differed from those used by adults migrating to wintering grounds (Chapters 2 and 4). The experienced birds were seemingly returning to known foraging sites (Naves et al. 2006; Regular et al. 2013; Chapter 2), whereas the naïve fledglings relied to an extent on external cues to navigate their unknown environment (Chapters 2 and 3). In particular, juvenile

movements were influenced by ocean surface winds, which presumably allow them to readily disperse from their natal site at low energetic cost (Weimerskirch et al. 2000b). As such, it seems likely that differences in wind conditions experienced by individuals during early life influence the routes and areas they will use as adults over their lifetime, as hypothesized for certain species of terrestrial birds; for instance honey buzzards (*Pernis apivorus*) and Spanish imperial eagles (*Aquila adalberti*) (Ferrer 1993; Vansteelant et al. 2017a).

As individuals acquire local information, movement strategies are also likely to be refined over successive months and years during the extended period of immaturity typical of long-lived species (Mueller et al. 2013; Sergio 2014; Merkle et al. 2019). In Chapter 3, I show that juvenile grey-headed albatrosses switch from travelling (fast and directed movement) to searching (slow and sinuous movement) in their second month at-sea, potentially indicative of an exploratory period during which foraging preferences are developed. However, as in many studies of juvenile behavior, the diminishing sample size prevented any further quantitative investigation of ontogenetic processes; indeed, for that reason, little is known about within-individual change in movement patterns in oceanic seabirds in general after their first year at sea (e. g. Åkesson & Weimerskirch 2005; de Grissac et al. 2017; Afan et al. 2019). While deployment and retrieval of geolocators that have been deployed long-term may eventually fill this knowledge gap, studies of shorter-lived species imply that individual experiences during early life; for instance of predators, competition, or habitats of varying quality, underpin the variety of behaviors observed in older life-stages (Groothuis et al. 2005; Stamps & Davis 2006; Urszán et al. 2018).

Therefore, a combination of environmental stochasticity and individual experience may drive movement patterns in the early years which persist over the lifetime of individuals. Nevertheless, it is likely that genetics also plays a role given studies of behavioral heritability in short-lived migratory species (e. g. passerines and insects; Pulido et al. 2001; Mouritsen et

al. 2013). Accordingly, juveniles tracked in Chapters 2 and 3 showed directed movement – consistent within, but not across species - during their first month at sea towards favorable foraging grounds, which suggests they may be navigating using an innate compass bearing (Yoda et al. 2017). This genetic mechanism is thought to serve as tool for guiding young which must learn to forage independently from their parents (de Grissac et al. 2016). As long-distance movement is central to the life-history adaptations of many animals, it could be that other traits of seabird movement have genetic components; e. g. dispersal distances or degree of exploratory behavior (Liedvogel et al. 2011). As it is challenging to follow movements of long-lived species over multiple generations, comparing the behaviors of related individuals (e. g. parents and offspring) may provide an important first step towards investigating this exciting question in behavioral ecology and establishing the extent to which strategies are fixed or flexible; this has important consequences for predicting whether species will be able to track changing environmental conditions (Beever et al. 2017).

7. 1. 2 Later life: factors underpinning variability in movements in mature individuals

Once individuals recruit into the breeding population, they are expected to be reasonably skilled foragers and have refined their movement strategies (Weimerskirch et al. 2005). However, in oceanic seabirds, new recruits still face new challenges in relation to breeding; mainly how to balance the acquisition of resources required for self-maintenance versus the body condition of their partners, particularly during incubation, and for provisioning a chick (Weimerskirch 1995; Collins et al. 2016). This balance can also change as the environment fluctuates in quality within and between years (Burke & Montevecchi 2009; Kowalczyk et al. 2015). As changing internal and external conditions are expected to influence individual movements (Nathan et al. 2008), there is considerable scope for seabirds to vary in their space use throughout the annual cycle, and over their lifetime, as they gain experience or experience changes in physiological condition (Weimerskirch et al. 2014; Elliott et al. 2014;

Phillips et al. 2017). Accordingly, in Chapter 5, I show that even in very productive habitats, breeding grey-headed and black-browed albatrosses (*Thalassarche melanophris*) show fine-scale differences in their foraging behavior, in this case related to age, sex and breeding stage

As South Georgia is home to very large populations of many other sympatric seabirds, niche theory stipulates that individuals should segregate in spatial, temporal or trophic axes, and that these observed behavioral differences may partially reflect strategies developed to reduce inter- and intra-specific competition for resources (Hutchinson 1957; Schoener 1971; Phillips et al. 2008). While this process potentially plays a fundamental role in structuring avian communities (Furness & Birkhead 1984; Lewis et al. 2001; Masello et al. 2010), our knowledge of patterns and dynamics of niche partitioning remains incomplete due to the multiple axes characterizing the so-called niche hyper-volume, and lack of data on the number and species of competitors at foraging sites (Wilson 2010; Wakefield et al. 2011; Clay et al. 2016). Concurrent deployment of video cameras and GPS loggers may provide some information the latter as well as fine-scale insights into avoidance behaviors (Thiebault et al. 2014). Regardless, more focus in the future on producing multi-species maps of foraging locations (using immersion data for instance), habitat use and changes in behavioral state during feeding trips would provide more general insights into the role of competition in structuring habitat use and decisions at finer-scales (i. e. integrated as a predictor variable in state-space models or integrated step-selection analysis), and throughout the annual cycle.

Finally, changing environmental conditions can alter the distribution and availability of resources and habitats, with impacts on foraging success, body condition and individual fitness if an animal cannot acquire enough resources, or must expend more energy (Chesson 1978; Pinaud et al. 2005; Kowalczyk et al. 2015). Hence, individuals are expected to show some degree of flexibility in their activity budgets and foraging behavior in order to survive and reproduce. In Chapter 5, I demonstrate that average at-sea activity patterns and foraging

range of adult albatrosses of two species varied among years. It, however, remains less clear which oceanographic or climatic features are driving these behavioral changes, and whether seabird species differ in the 'width' of their response; an ability which might separate winners from losers in light of climate change (Dingemanse & Wolf 2013). Existing evidence is complex as past seabird studies have demonstrated that species can show high individual consistency, or specialization, in certain aspects of their foraging behavior regardless of environmental conditions (e. g. regional wintering site fidelity) and large variation in other traits (e. g. migratory routes and staging areas) (reviewed in Phillips et al. 2017, but see Phillips et al. 2005; van Bemmelen et al. 2017). Responses may differ according to breeding status and even among populations of the same species (Hamer et al. 2001; Durant 2004; Delord et al. 2018). As such, further tracking at different breeding sites across multiple years would help tease apart the roles of habitat specialization and breeding constraints on the ability of individuals to adapt their movement strategies to environmental variation.

7. 2 Consequences of movement strategies for fisheries bycatch risk and conservation

7. 2. 1 Age-specific behavior and implications for assessing fisheries bycatch risk

Characterizing the diversity of behaviors exhibited by individuals and the drivers is essential to effectively manage wildlife populations and provide unbiased assessments of exposure to threats, particularly in long-lived species with age-structured populations (Williams et al. 2014; Carneiro et al. 2020; Elliott et al. 2020). In Chapters 2 and 4, I demonstrate its importance in the context of assessing fisheries bycatch risk, as juvenile white-chinned petrels and grey-headed albatrosses from Bird Island used different routes to adults, and consequently overlapped in distribution with other fishing fleets and in regions which had previously not been identified as high-risk areas (Clay et al. 2019). As the movements of naïve individuals reflect different processes (Chapters 2 and 3), it is likely that juveniles of other oceanic seabird species from South Georgia that are yet to be tracked (e. g. light-

mantled albatross, *Phoebetria palpebrata*) also differ in their distributions and potential bycatch risk from adults. Therefore, tracking through life-stages is highly recommended, particularly as improved distribution maps have successfully been used to inform conservation management, for instance via the design of no-take zones (Hays et al. 2019).

The relative spatial overlap of seabirds with the distribution of fishing effort corresponds fairly well with bycatch rates recorded by on-board observers, indicating that these ecological risk assessments reliably map bycatch risk at large spatial scales (Tuck et al. 2003; Phillips et al. 2006; Clay et al. 2019). However, there is evidence that overlap is scale-dependent and could be lower at finer spatial and temporal scales (i. e. birds use similar habitats as vessels but may not interact with gear; Torres et al. 2013). It is very clear that bycatch risk varies according to operational, meteorological or behavioral factors (Jiménez et al. 2012; Gianuca et al. 2017; Cortés et al. 2017). For instance, the deep-diving capabilities of white-chinned petrels likely expose them to higher bycatch risk, and these abilities should be taken into consideration when reviewing bycatch mitigation measures (Chapter 6). Gaps in age distributions are gradually being filled, improving large-scale overlap assessments at the population level, but efforts should also focus on examining how interactions with fishing vessels differ between individuals of varying sex, age etc. to provide more robust estimates of real, rather than potential risk (Collet et al. 2017). For instance, it is often suggested that juveniles are more vulnerable to bycatch due to their naïve foraging abilities (Gianuca et al. 2017). Robust investigations using new tracking devices which detect radar emissions would allow the relative attractiveness of vessels to be determined for birds of different ages, which could help with testing this hypothesis (Weimerskirch et al. 2020).

Bird-borne radar-detecting devices also show promise for filling in gaps in fishing effort related to the bycatch threat posed by illegal, unreported and unregulated fishing activities, which could be an important contributor of seabird population decline (Agnew et al. 2009;

Michael et al. 2017). Indeed, wandering albatrosses (*Diomedea exulans*) equipped with these loggers pick up radar signals emitted by undeclared fishing vessels, i.e., those not transmitting their location through the vessel Automatic Identification System (AIS) (Weimerskirch et al. 2018, 2020). A number of other technologies involving satellite tracking of vessels or the use of drones for marine surveillance are similarly paving the way for real-time and unbiased monitoring of many types of fishing activity (Kroodsma et al. 2018; Toonen & Bush 2020; Park et al. 2020). These tools may help ensure that fishing vessels and governments are held more accountable for their activities (Al-Abdulrazzak & Pauly 2014; Michelin et al. 2018), especially as documented breaches of regulations attract media attention (e. g. Hambling 2020; Patrick 2020; Roy 2020). This has the potential to influence public opinion and mobilize stakeholders, with important downstream effects on behavior and policy (Stark et al. 2018; Wu et al. 2018; Harasti et al. 2019).

7. 2. 2 Variation in behavior and general implications for marine spatial planning

In this thesis, I assess the susceptibility of my study species to fisheries bycatch; however, improved distribution maps of seabirds from South Georgia can also be used to understand the exposure of individuals to other threats such as plastic, oil or light pollution (Premier Oil Exploration & Production Limited 2015; Wilcox et al. 2015). In addition, as not all populations can be tracked due to logistical or financial reasons, refining our understanding of how individuals use their environment at one colony (as conducted in Chapter 6) could be useful for predicting marine habitat use of populations individuals colonies (e. g. Warwick-Evans et al. 2018). This is particularly relevant at South Georgia, where there are striking differences in population trends of albatrosses and giant petrels across the island group (Poncet et al. 2017, 2020; Rackete 2021). As distributions of animals are heterogeneous, particularly those of seabirds which typically have large ranges but aggregate in specific areas (Arcos et al. 2012; Christel et al. 2013; Carneiro et al. 2020), such analyses will help

with identifying the highest-density areas where the population is most at risk, and informing marine spatial planning (Lascelles et al. 2012; Tancell et al. 2016; Hindell et al. 2020). The transferability of habitat-use models to novel areas is highly variable (Torres et al. 2015; Yates et al. 2018; Péron et al. 2018). Further studies are therefore warranted that test the performance of different modelling approaches, as accuracy can possibly be improved. However, efforts should also focus on tracking from multiple sites to improve availability of data for inter-site comparisons.

Tracking can also serve to highlight potential variation in foraging behaviour and distribution that may underlie differences in individual quality, which has major implications for fitness and population trajectories. Indeed, in Chapter 6, I show that there are age-related differences in several aspects of albatross foraging behavior (landing rates, duration of foraging trips and habitat associations) and suggest that these are indicative of lower foraging efficiency in young and late adulthood. These age classes may thus be disproportionally affected by poor environmental conditions which reduce food availability (Oro et al. 2010; Haug et al. 2015; Fay et al. 2017). Future studies should focus on researching the link between foraging behavior, physiology and performance in more detail, i.e., tracking fitness (Crossin et al. 2014). For instance, deployment of stomach temperature sensors allows the timing and mass of ingested prey to be determined over the course of a foraging trip (Weimerskirch et al. 2005). Determining whether individuals vary significantly in their foraging success or efficiency should help reveal the mechanisms by which environmental variability affects population dynamics. This information could be used to develop process-based models which predict how populations may respond to worrying scenarios of global warming and test different management scenarios (e. g. via agent-based modelling; McLane et al. 2011; Beltran et al. 2017).

7. 3 Next steps in movement ecology and protecting wide-ranging species

7. 3. 1 Bridging the gap between movement and fitness

Throughout the previous chapters, I have demonstrated how tracking technologies can be used to uncover the incredible capacity and varying motivations for individual movement, but the consequences of observed strategies for fitness (i. e. what constitutes a good or poor strategy) represents a crucial knowledge gap that is challenging to address (Morales et al. 2010; Matthiopoulos et al. 2015; Hays et al. 2016). Indeed, determining the costs and benefits of different movement patterns is complex, as some metrics of performance are difficult to measure non-invasively, or for logistical or other reasons (e. g. energy expenditure or lifetime reproductive output McGraw & Caswell 1996; Furness & Bryant 1996). The consequences of different movement strategies for fitness may not be immediately observable (e. g. carry-over effects from the non-breeding season; Fayet et al. 2016). As a result, past studies have focused on characterizing the fitness consequences of isolated or a small number of events, such as a series of dives or foraging trips (Boyd et al. 1997; Weimerskirch 1998; Bradshaw et al. 2007). However, the advent of accelerometers (Yoda et al. 2001; Watanabe et al. 2005) is paving the way for assessments of the energetic costs and benefits of larger scale or long-term movements (e. g. outward vs. return foraging flights) as these devices provide an index of activity-specific energy expenditure in the field; a key metric linking behavior and overall fitness (Wilson et al. 2006; Grémillet et al. 2018a; Pagano & Williams 2019).

Oceanic seabirds in the marine environment provide a great study system for developing this research field as their movement strategies differ along a number of behavioral axes (foraging trip duration, landing rates, habitat associations, diving depths etc.), suggesting there are a multitude of mechanisms used by individuals to adjust their energy budgets (Ropert-Coudert et al. 2004; Fort et al. 2013; Dunn et al. 2020). Furthermore, fitness-related metrics (e. g. breeding success) are relatively easy to measure at breeding colonies so there is the

possibility of determining energetic thresholds over which deleterious effects are observable at individual and potentially population levels (Welcker et al. 2009a). In addition to advancing our ecological understanding of optimal movement strategies (Gleiss et al. 2011), this research informs conservation efforts, particularly with regards to (1) diagnosing mechanisms responsible for driving population trends (Pichegru et al. 2007), (2) informing ecological risk assessments of offshore developments which might displace individuals from high-quality habitats (Masden et al. 2010) and (3) predicting whether individuals will be able to cope with changing environmental conditions (Clairbaux et al. 2019).

7. 3. 2 Assessing dynamic exposure to impacts and facilitating collaboration

The urgency of assessing the vulnerability of highly mobile species to human activities and climate change will only increase as environmental conditions worsen and the human footprint expands (Runge et al. 2014). Many studies use tracking data in risk assessments which are static in their nature (e. g. Fossette et al. 2014; Queiroz et al. 2019; Aschettino et al. 2020), and which, in turn, have informed static management strategies such as the creation of fixed marine protected areas (Hyrenbach et al. 2000). Such strategies have reduced some pressures associated with marine resource exploitation particularly if they impact critical habitats and threatened species (Pichegru et al. 2010; Gormley et al. 2012). However, emerging dynamic assessment and management tools may provide more promising avenues for protecting mobile individuals as they address the variability inherent in oceanic systems (reviewed in Lewison et al. 2015). For instance, the TurtleWatch product provides up-to-date information to longline fishers of areas to avoid to reduce bycatch based on the predicted thermal habitat of loggerhead sea turtles (*Caretta caretta*) in the Pacific Ocean (https://oceanwatch.pifsc.noaa.gov/turtlewatch.html; Howell et al. 2008), and similar methods could be trialed for other marine megafauna based on their habitat preferences.

As resources available for research and conservation are often limited, it is essential that risk assessments move towards integrating multiple species in order to more effectively prioritize conservation approaches in time and space which benefit habitats key to the survival of many individuals. As such, studies which identify hotspots used by multiple species are increasing (Clay et al. 2019; Queiroz et al. 2019; Hindell et al. 2020); however, there are some barriers hampering the widespread generation of such maps. Firstly, as distribution data can be collected using a wide range of methods (tracking devices, traditional surveys, satellite imagery, drones), it is essential that rigorous protocols are developed to standardize these diverse data types and improve spatial, temporal and taxa coverage (e. g. similarly to Waggitt et al. 2020). Secondly, increased efforts to make tracking data publicly available once published, instead of available only by request, may facilitate access for a wider range of stakeholders with varying research and management aims (e. g. similarly to the International Union for Conservation of Nature Species Range maps; https://www.iucnredlist.org/resources/spatial-data-download). Effective collaboration is paramount for achieving these aims, as wide-ranging species cross jurisdictional borders, tracking data is collected by many different institutions, and management is the responsibility of multiple national and international bodies (Kark et al. 2015; Hays et al. 2019; Beal et al. 2021).

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Appendix 1 – Supplementary material for chapter 2

S1. 1 Tracking data processing (geolocators)

In order to estimate locations for adults tracked during the non-breeding season, twilight events were first estimated using the raw light intensities from the geolocators using the function 'preprocessLight' in the 'TwGeos' package, with a threshold setting of 2 lux, an offset of 12 hours and a maximum light level of 74418.6 lux. Locations were then computed from the twilight events using the 'prob_algorithm' function in the 'probGLS' package (Merkel et al. 2016). This function uses an iterative, forward-step-selection, probabilistic algorithm that incorporates information on various sources of uncertainty, the behaviour of the study species, and the characteristics of the environment to generate the most likely movement path (Table S1.1). Two locations were generated per day with a median error of up to 185 km (Merkel et al. 2016). Resulting points were removed if they required unrealistic flight speeds (>35 km.h-1 sustained over a 48 h period; Phillips et al. 2004a), or the bird to cross land.

Table S1. 1: ProbGLS algorithm parameters used to estimate locations of non-breeding adult white-chinned petrels from twilight events. Adults were tracked from Bird Island (South Georgia) during winter 2015 using Global Location Sensors (GLS).

Model parameter	Description	Value used
particle.number	Number of particles computed for each point cloud	10 000[a]
Iteration.number	Number of track iterations	200[a]
sunrise.sd & sunset.sd	Shape, scale and delay values describing the assumed uncertainty structure for each twilight event using a log-normal distribution	2.49/0.94/0[a]
range.solar	Range of solar angles used	-7° to -1°[a]
boundary.box	The range of longitudes and latitudes likely to be used by tracked individuals	Lon (-100°, 10°) & Lat (-80°, 0°)[b]
days.around.spring.equinox & days.around.fall.equinox	Number of days before and after an equinox event in which a random latitude will be assigned	14/21 (spring) & 21/14 (fall)[c]
speed.dry	Fastest most likely speed, speed standard deviation and maximum speed allowed when the logger is not submerged in sea water	10.23/3.72/17.94 $m.s^{-1}$ [d]
speed.wet	Fastest most likely speed, speed standard deviation and maximum speed allowed when the logger is submerged in sea water	0.78/1.09/3.56 $m.s^{-1}$ [d]
sst.sd	Logger-derived sea surface temperature (SST) sd	0.5°C [e]
max.sst.diff	Maximum tolerance in SST variation	3°C [a]
east.west.comp	Compute longitudinal movement compensation for each set of twilight events	Used[a]

[a] Same values as in Merkel et al. (2016), which involved the same geolocator model and similar foraging areas as in this study (South Georgia and Patagonian Shelf)

[b] Encompasses southwest Atlantic, Patagonian Shelf and west coast of South America (Phillips et al. 2006)

[c] Number of days chosen following Fox (2009)

[d] Calculated from GPS tracks and associated immersion data from breeding adults

[e] Logger-temperature accuracy

S1. 2 Utilisation distributions

a) Utilisation distributions – determining minimum population sizes

In order to determine whether sample sizes were sufficient to represent the population-level distribution in each week for each life-history stage, a resampling procedure was used that iteratively calculated the core and general use areas for an increasing number of individuals, selected at random, 1,000 times (500 times for week 6 for juveniles, given the small sample size; see below), without replacement. Four non-linear models were fitted to resampled outputs; the two- and three-parameter Michaelis-Menten and the two- and three- parameter asymptotic exponential models within the R package 'drc' (Ritz. & Strebig 2016), as previous studies have indicated that the area occupied reaches an asymptote once a certain number of individuals are included (Hindell et al. 2003; Soanes et al. 2013). Models were then ranked according to Akaike Information Criterion (AIC) to determine which model fitted the resampled data best (Table S1.2a and b). The 3-parameter Michaelis-Menten model performed best overall (71% of all combinations) and was therefore adopted for all datasets in order to provide a standardised method for prediction and comparison of minimum sample sizes.

For each stage-week combination, the core and general use areas were then extrapolated to a 'colony' size of 50 individuals, as it is rare for more birds to be tracked in a particular breeding stage in any given year. Sufficient individuals were considered to have been tracked at a cut-off of 95% of the core and general use areas predicted for 50 individuals. This resampling procedure was applied to each stage-week combination up to week 6 (Table S1.3, example in Figure S1.1), as juvenile sample sizes for weeks 7-8 were deemed too small for this analysis (<= 5 individuals tracked).

Table S1. 2: Ranking of models used to determine the relationship between sample size and home range area for juvenile and non-breeding adult white-chinned petrels tracked from Bird Island (South Georgia) during the 2014/15 breeding season and subsequent winter, according to AIC. Best models for each week for the two life-history stages (juveniles and non-breeding adults) are in blue. Models compared using AIC are the two- and three- parameter asymptotic exponential models (2A and 3A respectively), and the two- and three- parameter Michaelis-Menten asymptotic exponential models (2MM and 3MM respectively).

a) Core

		1) Juveniles				2) Non-breeding adults			
Week	**Iterations**	**2A**	**3A**	**2MM**	**3MM**	**2A**	**3A**	**2MM**	**3MM**
1	1,000	286.3	**284.6**	299.6	293.9	512.6	**491.4**	494.7	493.1
2	1,000	247.9	242.4	232.3	**230.1**	509.9	499.0	491.1	**480.0**
3	1,000	248.2	**235.6**	236.3	236.5	504.2	490.3	488.3	**466.8**
4	1,000	207.4	**203.9**	222.6	208.5	495.5	**469.6**	503.1	489.5
5	1,000	224.3	209.2	**196.2**	198.2	523.2	496.0	452.1	**451.7**
6	500 (1) and 1,000 (2)	150.7	150.9	150.1	**145.5**	537.0	514.4	494.7	**484.6**

b) General

		1) Juveniles				2) Non-breeding adults			
Week	**Iterations**	**2A**	**3A**	**2MM**	**3MM**	**2A**	**3A**	**2MM**	**3MM**
1	1,000	317.0	303.5	300.5	**286.3**	587.6	553.4	569.8	**540.7**
2	1,000	261.8	263.6	271.0	**235.6**	580.8	551.7	561.2	**538.3**
3	1,000	257.6	258.3	266.6	**252.0**	580.3	551.5	558.8	**537.6**
4	1,000	237.7	232.0	227.1	**212.9**	580.8	549.2	554.4	**529.3**
5	1,000	240.4	222.8	**214.0**	215.2	575.2	547.1	527.0	**495.0**
6	500 (1) and 1,000 (2)	164.4	146.9	152.9	**145.8**	576.5	537.6	534.8	**498.9**

Table S1. 3: Weekly observed and minimum predicted sample sizes for juvenile and non-breeding adult white-chinned petrels tracked from Bird Island (South Georgia) during winter 2015. Minimum sample sizes with 95% confidence intervals are in parentheses. Predictions are for a 'colony' size of 50 individuals.

Week	Stage	Sample size	Minimum number predicted	
			61%	95%
1	**JUV**	11	22 (15 – 40)	20 (17 – 22)
	NB	16	17 (13 – 22)	33 (27 – 42)
2	**JUV**	8	33 (29 – 38)	28 (27 – 30)
	NB	16	16 (14 – 20)	33 (27 – 42)
3	**JUV**	8	35 (29 – 44)	30 (25 – 35)
	NB	16	17 (15 – 19)	31 (25 – 40)
4	**JUV**	8	14 (10 – 23)	21 (18 – 25)
	NB	16	15 (12 – 18)	28 (24 – 34)
5	**JUV**	7	17 (13 – 23)	16 (12 – 22)
	NB	16	20 (19 – 21)	26 (25 – 27)
6	**JUV**	6	11 (4-22)	9 (6-17)
	NB	16	26 (23-30)	27 (26-29)

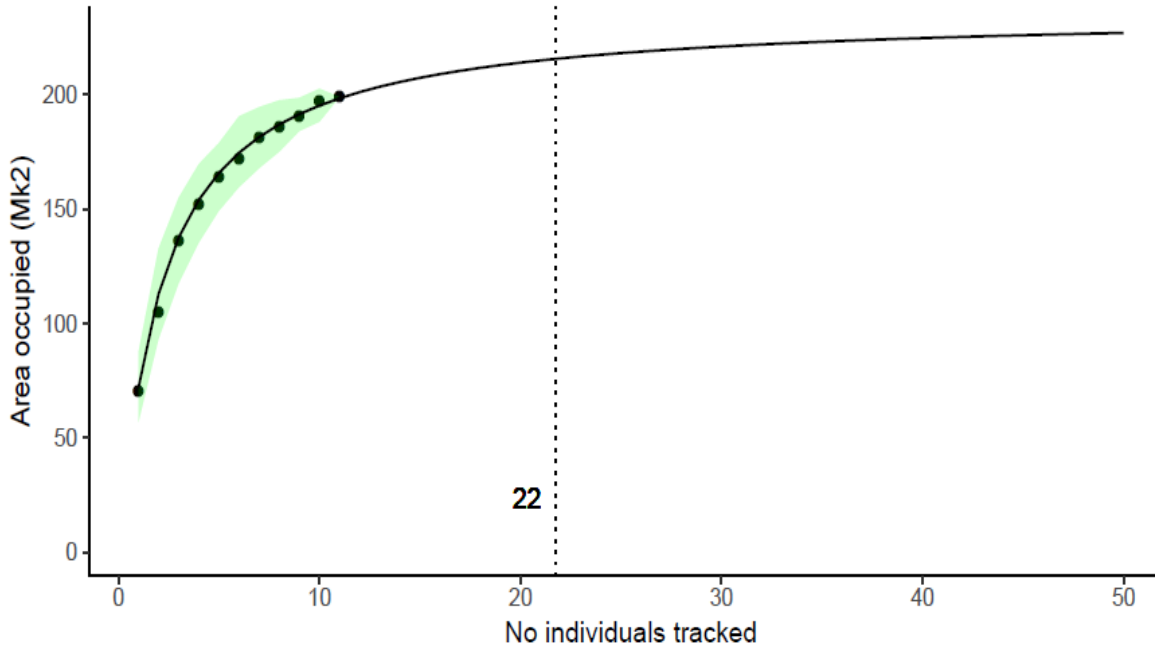

Figure S1.1: Core area as a function of sample size for juvenile white-chinned petrels in week 1 post-fledging. The fitted asymptotic relationship (three-parameter Michaelis-Menten; black line), median area occupied (black points), and 25% and 75% quantiles (coloured, shaded polygon) of 1,000 resample iterations are shown for the core use area (61%). The predicted minimum sample size is shown by the dashed vertical line.

b) Utilisation distributions – determining appropriate core level

Core areas were delineated following Vander Wal & Rodgers (2012), using a time-maximizing function derived from kernel analyses. Increase in utilization distribution area was plotted against increasing isopleth level. An exponential regression curve was then fitted to the data, and the isopleth value at which the slope of the line fitted to the data was equal to 1 when differentiated was considered to define the boundary of the core area. This point represents a threshold where the proportional home range area begins to increase at a greater rate than the probability of use (see example in Figure S1.2). This procedure was repeated for all individuals within each unique stage-week combination, and the mean determined core isopleth level, 61%, was used for all subsequent analyses (Table S1.4).

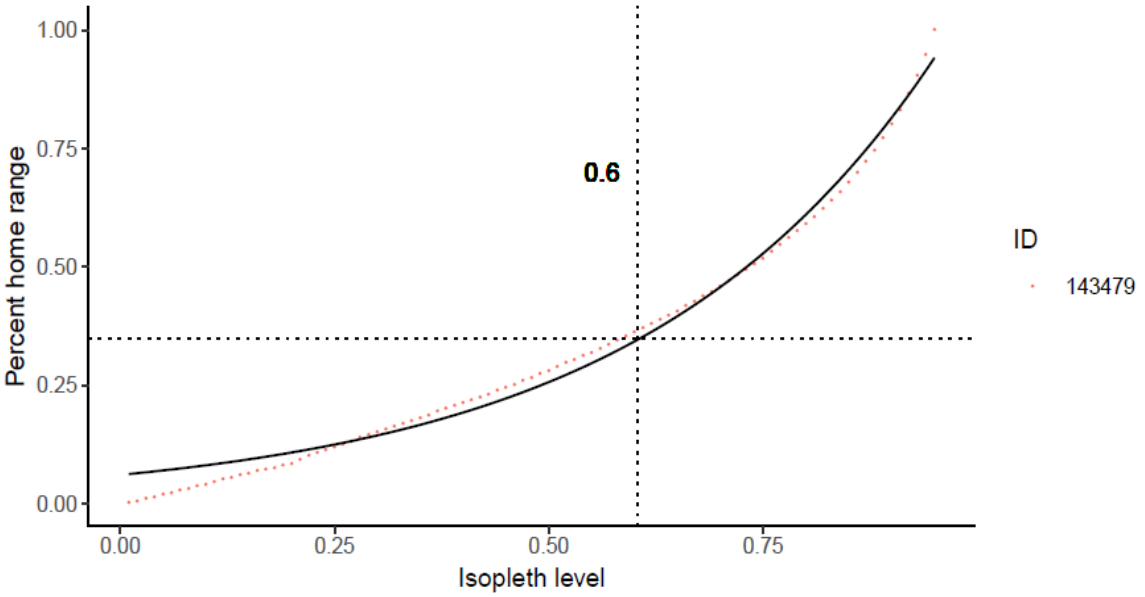

Figure S1.2: Example of delineating core areas of space use according to Vander Wal & Rodgers (2012). Increasing utilization distribution area is plotted as percent of the individual home range against increasing isopleth levels (Bird ID: 143479, red points). The solid curve is the exponential regression equation fitted to the data. The intersection of the dashed lines indicate the threshold (slope=1) where area under the curve in the lower left quadrant is core area. The corresponding core isopleth value is indicated in bold.

b) Utilisation distributions – calculating overlap in core and general use areas

I used Bhattacharrya's affinity (BA) to calculate the observed overlap in core and general-use area between stages for each week using the function 'kerneloverlap' in the R package 'adehabitatHR' (Calenge 2006), as it is considered the most appropriate measure for quantifying similarity among UD estimates (Fieberg & Kochanny 2005). BA estimates range between 0 and 1, representing no similarity between UDs (i.e. no overlap) and identical UDs

(complete overlap), respectively. A randomization procedure was used to test the null hypothesis that there was no difference in their spatial distribution. To test for differences between juveniles and adults, bird identities were randomly reassigned without replacement and overlap scores were calculated for 1000 iterations, maintaining the same observed ratios. P-values were determined as the proportion of randomized overlaps that were smaller than the observed (Breed et al. 2006).

Table S1. 4: Mean ± standard deviation of core isopleth levels determined for each week for juvenile and non-breeding adult white-chinned petrels tracked from Bird Island (South Georgia) during winter 2015.

	Juveniles		**Non-breeding adults**	
Week	*Sample size*	*Core isopleth level*	*Sample size*	*Core isopleth level*
1	11	0.60 ± 0.003	16	0.62 ± 0.010
2	8	0.61 ± 0.006	16	0.62 ± 0.007
3	8	0.61 ± 0.006	16	0.62 ± 0.009
4	7	0.61 ± 0.007	16	0.62 ± 0.009
5	7	0.61 ± 0.005	16	0.62 ± 0.010
6	5	0.61 ± 0.001	16	0.62 ± 0.010
7	3	0.61 ± 0.001	16	0.61 ± 0.008
8	2	0.61 ± 0.003	16	0.61 ± 0.007
	Overall average core level			**0.61**

S1. 3 Wind datasets

a) Comparing monthly Copernicus and NOAA blended winds products

I determined whether the two wind datasets (NOAA blended winds [https://www.ncei.noaa.gov/thredds/catalog/uv/monthly/catalog.html; Zhang et al. 2006]; SCATterometer [ASCAT] scatterometer onboard METOP-A and METOP-B satellites [Downloaded from Copernicus; WIND_GLO_WIND_L4_REP_OBSERVATIONS_012_003; https://resources.marine.copernicus.eu/; Bentamy & Fillon, 2012]) differed for years when both were available (2008-2011) and whether this affected mechanistic model simulations. Differences in wind speed between the two datasets in months corresponding to our main study period (April-June) were minimal and restricted to the most southerly latitudes, and the west coast of South America (Fig S1.3a). There were some differences in wind direction between the datasets along the boundary separating the prevailing westerlies from the trade winds (Fig S1.3b). However, running model simulations using each dataset produced very similar results for a=0.2 (the scenario which was most likely to have been influenced by these differences), suggesting there was no material influence on model simulations (Fig S1.3c).

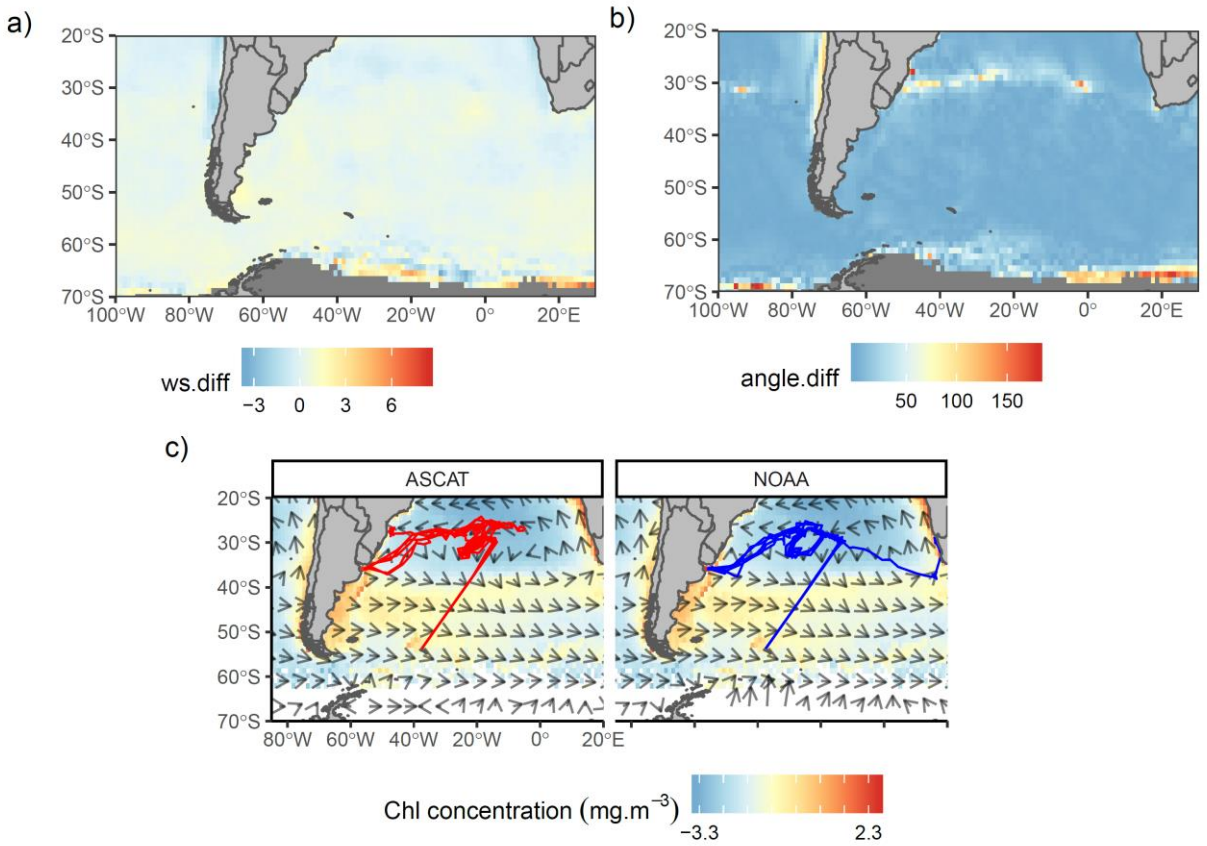

Figure S1. 3: Difference in a) mean wind speed (ws.diff), and b) mean wind direction (angle.diff) averaged over April-June 2008-2011, calculated using zonal and meridional wind products from NOAA (monthly blended winds) and ASCAT (WIND_GLO_WIND_L4_REP_OBSERVATIONS _012_003) c) Outputs from the mechanistic movement model for *a* = 0.2 over the months of April-June. Simulations were run six times using ASCAT and NOAA zonal and meridional wind products, respectively. Chlorophyll *a* concentration was log transformed.

S1. 4 Tracking metadata

Table S1. 5: Deployment and tracking metadata for juvenile and non-breeding white-chinned petrels tracked from Bird Island (South Georgia) in the 2014/15 breeding season and subsequent winter. PTT – Platform Terminal Transmitter; GLS – Global Location Sensor; GPS - Global Positioning System logger.

Stage	Device	Sample size	Date of 1st location	Date of last location
Juvenile	PTT	13	15-Apr-2015	05-Jul-2015
Non-breeding adults	GLS	16	23-Jan-2015	07-Nov-2015
Incubating adults	GPS	12	23-Dec-2014	22-Jan-2015

Table S1. 6: Number of juvenile white-chinned petrels tracked per week since fledging from Bird Island (South Georgia) in 2015.

Week	1	2	3	4	5	6	7	8
Sample size	13	8	8	8	7	6	4	2

S1. 5 Model selection table

Table S1. 7: Model selection table showing all possible combinations of predictors for linear mixed-effect models investigating differences in a) movement metrics of adult (non-breeding, NB and incubating, INC) and juvenile (JUV) white-chinned petrels, and b) overlap of the core distribution of NB and JUV birds with demersal and pelagic longline fishing effort. All birds were tracked from Bird Island (South Georgia) during the 2014/15 breeding season and subsequent winter. Models were ranked according to Akaike Information Criterion (AICc) and the best-supported model(s) were considered to be those within 2Δ AICc of the top model, and are highlighted in blue. ‘‘Life-history stages considered’ indicates the life-history stages compared for a given movement metric; predictor variables retained in the best models are denoted with an ‘x’; variables that were not modelled with ‘NA’; ‘df’ is the degrees of freedom; ‘Week’ the weeks following departure from the colony; and ‘AICcw’ the AICc weight, the relative probability that a given model is the best model.

		Predictor variables							
Life-history stages considered	**Metrics**	Intercept	Life-history stage	Week	Life-history stage: Week	**df**	**AICc**	**ΔAICc**	**AICcw**
c) MOVEMENT METRICS									
NB vs. JUV	Maximum range (km)	x	x	x	x	18	2417	0.000	1.000
		x	x	x		11	2514	96.64	0.000
		x		x		10	2549	131.2	0.000
		x	x			4	2772	354.8	0.000
		x				3	2798	380.3	0.000
NB vs. JUV	Longitude (°)	x	x	x	x	18	1107	0.000	1.000
		x	x	x		11	1171	64.81	0.000
		x		x		10	1207	100.1	0.000
		x	x			4	1288	181.8	0.000
		x				3	1328	221.3	0.000

Table S1. 7 continued

Life-history stages considered	Metrics	Predictor variables				df	AICc	ΔAICc	AICcw
		Intercept	Life-history stage	Week	Life-history stage: Week				
INC vs. JUV	Speed ($km.hr^{-1}$)	x	x	NA	NA	4	901.5	0.000	0.654
		x				3	902.8	1.272	0.346
INC vs. JUV	Sinuosity	x		NA	NA	3	2.082	0.000	0.857
		x	x	NA	NA	4	5.669	3.587	0.143
JUV	Speed ($km.hr^{-1}$)	x	NA		NA	3	158.4	0.000	1.000
		x	NA	x	NA	10	172.9	14.47	<0.001
JUV	Sinuosity	x	NA		NA	3	-25.54	0.000	1.000
		x	NA	x	NA	10	-1.026	24.52	0.000
d) OVERLAP METRIC									
NB vs. JUV	Overlap score ($hours.week^{-1}$)	x	x	x	x	18	901.4	0.000	1.000
		x	x	x		11	950.7	49.25	0.000
		x		x		10	976.3	74.93	0.000
		x	x			4	981.5	80.07	0.000
		x				3	1004	102.6	0.000

S1. 6 Mechanistic movement model

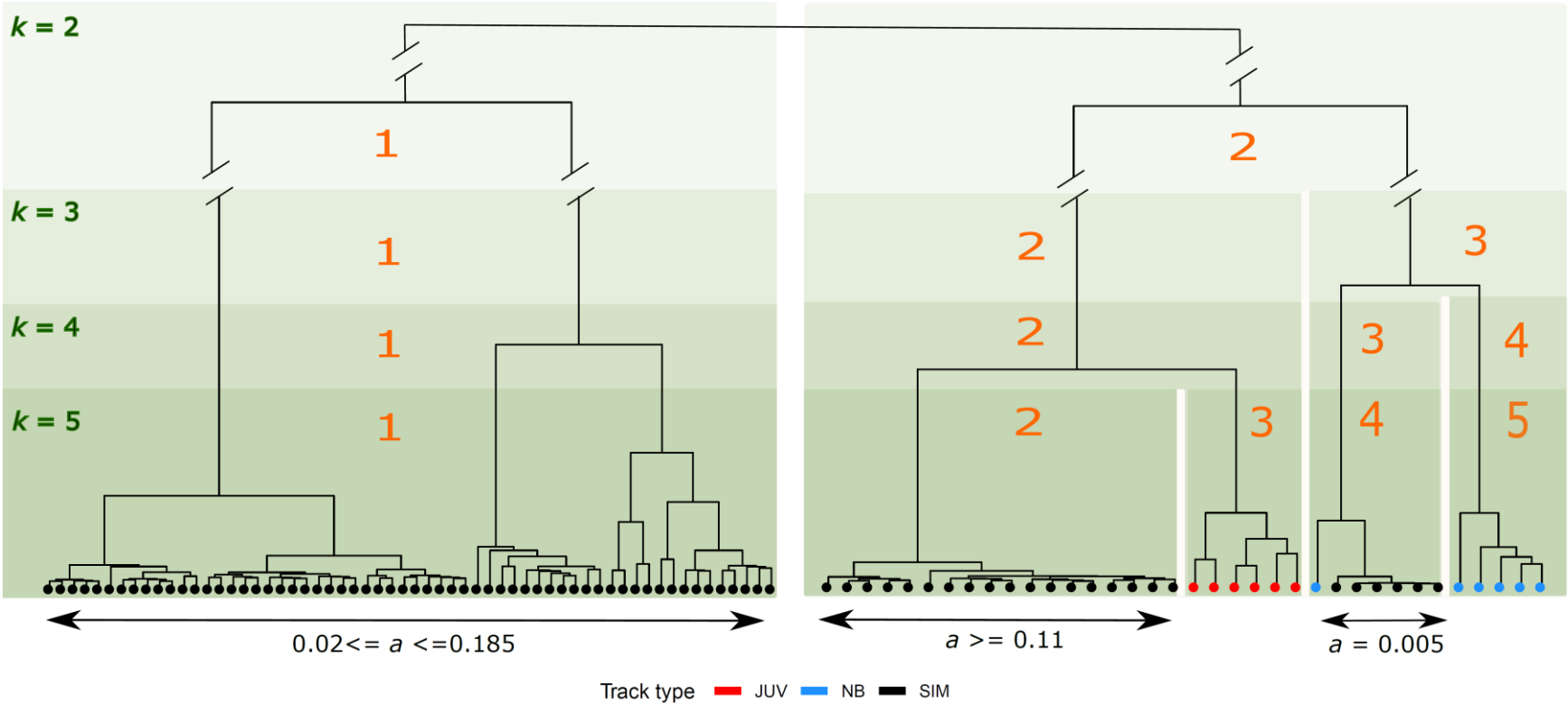

Figure S1. 4: Full hierarchical clustering of simulated (SIM) and observed tracks (JUV= Juvenile, NB=Non-breeding adults) for an increasing number of cluster groups *k*. White bars delineate clusters and orange numbers indicate cluster number for each value of *k*. Background shading darkens in colour for an increasing value of *k*. Coloured dots show to which stage each grouped track belongs (juvenile, non-breeding adult, and simulated). Simulations were run for values of *a* as multiples of 0.015 from 0.005 to

Appendix 2 - Supplementary material for chapter 3

S2. 1 Tracking data sample sizes and monthly movements

Table S2. 1: Monthly sample size of tracked juvenile grey-headed albatrosses from Bird Island (South Georgia) in 2018 and 2019 using Platform Terminal Transmitters (PTTs).

Month since fledging	2018	2019	Total
1	9	14	23
2	9	11	20
3	8	8	16
4	5	7	12
5	2	4	6
6	2	2	4
7	1	0	1

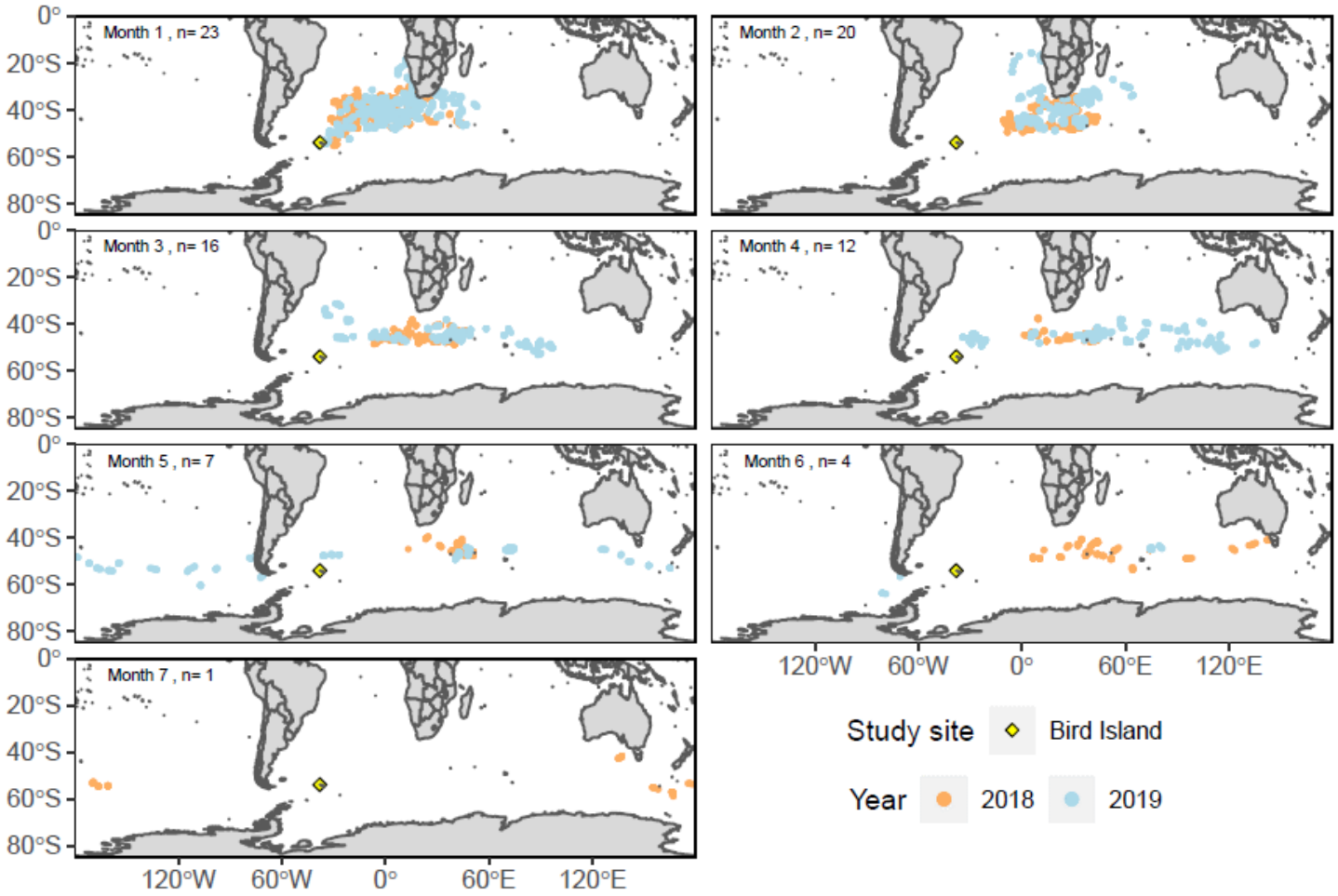

Figure S2. 1: Monthly at-sea distribution of juvenile grey-headed albatrosses tracked from Bird Island (South Georgia) in 2018 (n=9) and 2019 (n=14) using platform terminal transmitters (PTTs

S2. 2 Yearly and diurnal variation in movement characteristics

Table S2. 2: Comparison of movement characteristics (step lengths and turning angles) between 1) tracking year and 2) daylight and darkness for juvenile grey-headed albatrosses tracked from Bird Island (South Georgia) in 2018 (n=9) and 2019 (n=14). Significant comparisons ($p<0.05$) are in bold and sample mean and standard deviations of turning angles were computed using circular statistics within package 'circular' (Lund et al. 2017).

Movement metric	**Sample size**	**Sample mean ± standard deviation**		**Statistical test**	**Test results**
		2018	*2019*		
Step length ($km.hr^{-1}$)	7333	14.5 ± 15.9	15.2 ± 16.8	Unpaired two-sample Wilcoxon test	W=6559531, p=0.216
Turning angle (radians)	6430	<-0.01 ± 1.18	0.01 ± 1.28	Watson's two-sample test of homogeneity	**t=0.2697, p<0.01**
		Daylight	*Darkness*		
Step length ($km.hr^{-1}$)	7333	23.7 ± 18.1	9.12 ± 12.1	Unpaired two-sample Wilcoxon test	**W=10155039, p<0.001**
Turning angle (radians)	6430	0.01 ± 1.06	<0.01 ± 1.35	Watson's two-sample test of homogeneity	**t=3.1672, p<0.001**

To determine whether the movement characteristics of juvenile grey-headed albatrosses tracked from Bird Island, South Georgia, differed between tracking years, I used an unpaired two-sample Wilcoxon test and Watson's two-sample test of homogeneity to compare the distribution of step lengths and turning angles respectively, over the first four months post-fledging between 2018 and 2019. There was no significant difference between years in terms of step lengths (Table S2. 2 and Figure 2. 2Sa), and while birds travelled on average in a significantly more directed manner in 2018 than in 2019, this difference was visually minimal

(Table S2. 2 and Figure S2. 2b), and therefore tracking data from 2018 and 2019 were pooled for subsequent integrated step-selection analysis (*i*SSA). Using the same tests as above, I furthermore contrasted the distribution of step lengths and turning angles between daylight and darkness. Birds moved significantly faster and in a more directed manner on average during daylight and I therefore excluded movements which occurred during darkness from the *i*SSA as it was assumed that travel and foraging behaviours were minimal during this time period (Table S2. 2 and Figure S2. 2 c & d).

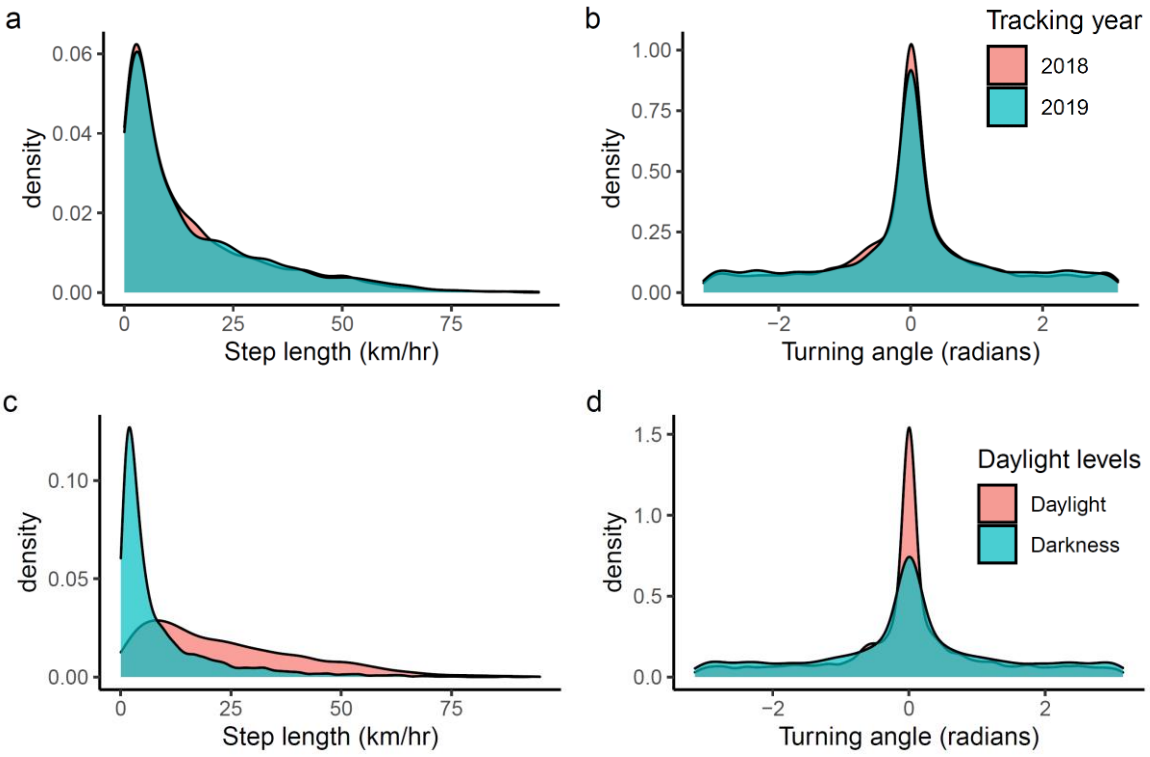

Figure S2. 2: Variation in step lengths and turning angles between tracking years (a & b), and between daylight and darkness (c & d) of juvenile grey-headed albatrosses tracked from Bird Island (South Georgia) in 2018 (n=9) and 2019 (n=14).

S2. 3 Determining appropriate number of random steps

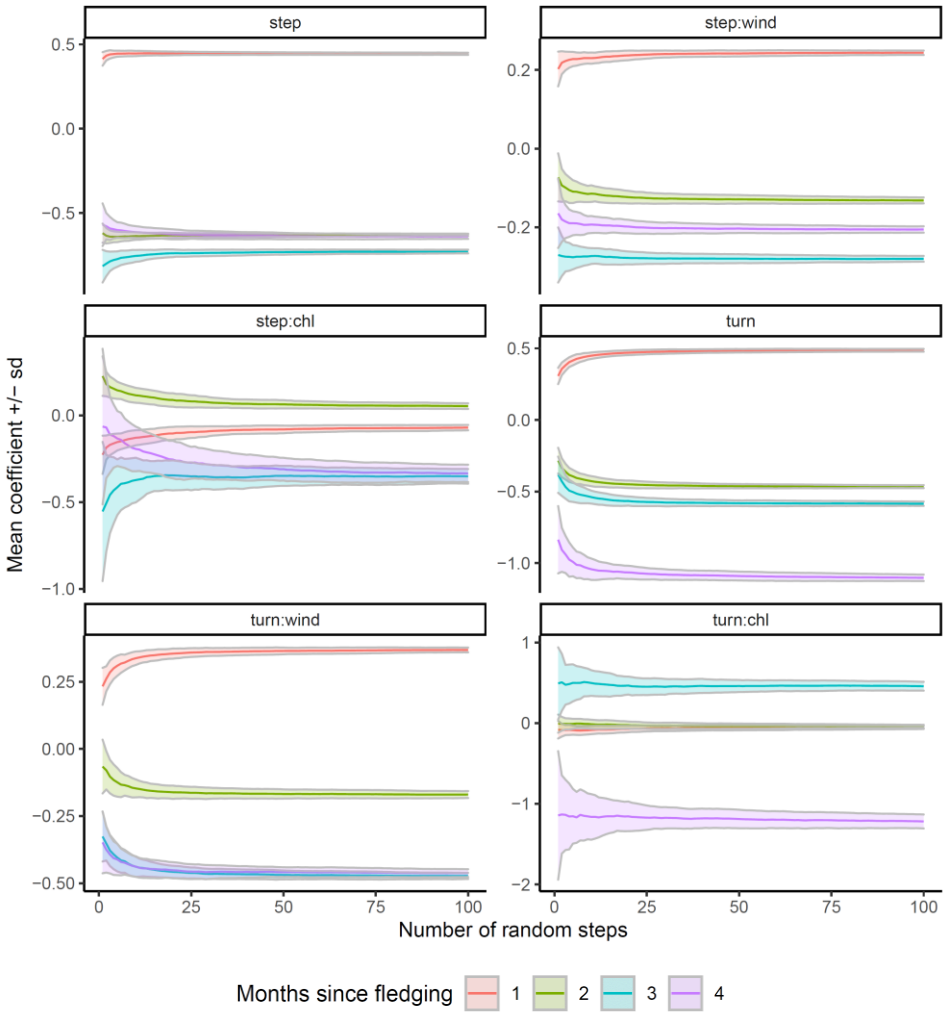

Figure S2. 3: Mean coefficient value of parameters for an increasing number of random steps (between 1 and 100) included in the integrated step-selection analysis investigating the effect of environmental conditions (wind speeds 'wind' and chlorophyll concentration 'chl' as a proxy for prey resources) and time (months since fledging 'month') on the movement characteristics (step length 'step' and turning angle 'turn') of juvenile grey-headed albatrosses tracked from Bird Island (South Georgia) in 2018 and 2019. Models were fitted 100 times and shaded areas represent standard deviations of parameter coefficients for an increasing number of random steps.

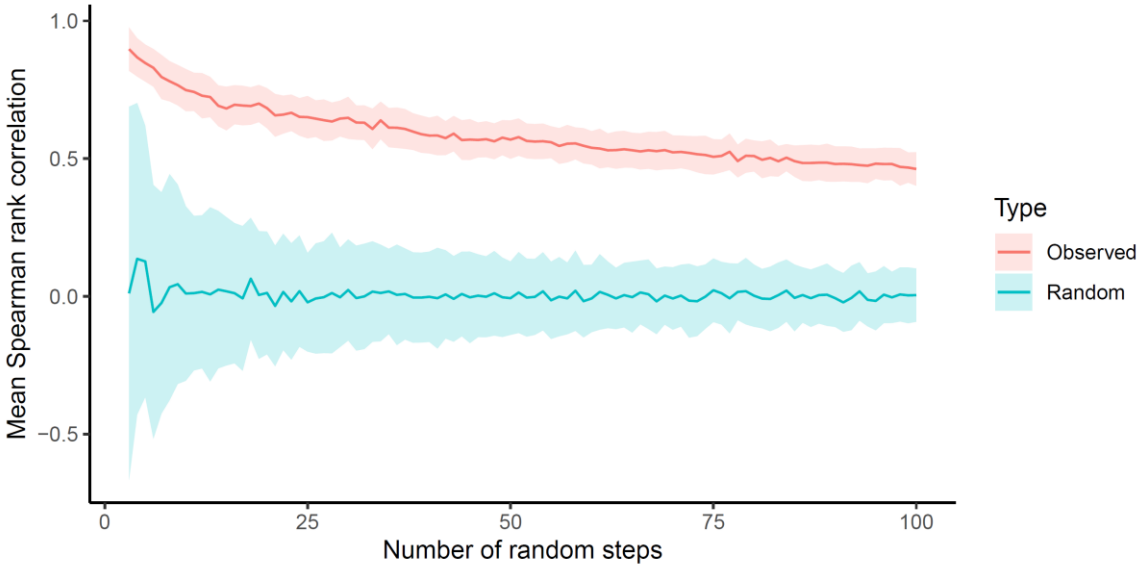

Figure S2. 4: Goodness of fit for an increasing number of random steps (between 3 and 100) of integrated step-selection analysis investigating the effect of environmental conditions (wind speeds 'wind' and chlorophyll concentration 'chl' as a proxy for prey resources) and time (months since fledging 'month') on the movement characteristics (step length 'step' and turning angle 'turn') of juvenile grey-headed albatrosses tracked from Bird Island (South Georgia) in 2018 and 2019. Fit was assessed using *k*-fold cross-validation adapted for conditional logistic regression repeated 100 times, and yielded an average Spearman rank correlation and 95% confidence intervals (shaded areas) for observed r_{obs} and random steps r_{rand}. Robust models are considered to have high r_{obs} relative to r_{rand}.

S2. 4 Integrated step-selection model selection table (for models with weight > 0.01)

Table S2. 3: Model selection table for integrated step-selection analysis investigating the effects of winds ('wind'), chlorophyll concentration (a proxy for prey resources; 'chl') and time (months since fledging; 'month') on the movement characteristics (step lengths; 'step', and turning angles; 'turn') of juvenile grey-headed albatrosses tracked from Bird Island (South Georgia) in 2018 (n=9) and 2019 (n=14) using Platform Terminal Transmitters (PTTs). Models including all possible combinations of predictor variables were considered and ranked according to Akaike information criterion (AIC). Predictor coefficients and 95% confidence intervals (in brackets) are shown for predictor variables retained in top models, and variables for which confidence intervals did not contain 0 are considered to have a significant effect on movement characteristics (shown in blue). 'df' are degrees of freedom, and 'weight' the relative probability that a given model is the best model.

		Predictors									
Model #	**month**	**step**	**step:chl**	**step:wind**	**turn**	**turn:chl**	**turn:wind**	**df**	**AIC**	**ΔAIC**	**weight**
1	1/overall	0.44 (0.36, 0.53)	-0.06 (-0.11, -0.01)	0.25 (0.16, 0.33)	0.49 (0.33, 0.65)	-0.02 (-0.13, 0.08)	0.38 (0.21, 0.54)	24	19358	0.00	0.42
	2	-0.65 (-0.76, -0.54)	0.06 (-0.01, 0.14)	-0.12 (-0.23, -0.01)	-0.45 (-0.67, -0.23)	-0.10 (-0.24, 0.04)	-0.20 (-0.42, 0.02)				
	3	-0.75 (-0.89, -0.62)	-0.45 (-0.90, 0.01)	-0.29 (-0.40, -0.18)	-0.59 (-0.88, -0.31)	0.49 (-0.45, 1.42)	-0.47 (-0.69, -0.25)				
	4	-0.64 (-0.82, -0.45)	-0.31 (-0.90, 0.28)	-0.20 (-0.33, -0.07)	-1.09 (-1.42, -0.76)	-1.21 (-2.28, -0.14)	-0.46 (-0.70, -0.21)				
2	1/overall	0.44 (0.36, 0.53)	-0.06 (-0.11, <-0.01)	0.25 (0.16, 0.33)	0.49 (0.33, 0.66)	-0.08 (-0.15, -0.01)	0.36 (0.20, 0.52)	21	19359	1.58	0.31
	2	-0.65 (-0.76, -0.54)	0.06 (-0.01, 0.13)	-0.12 (-0.23, -0.01)	-0.47 (-0.69, -0.25)		-0.18 (-0.39, 0.04)				
	3	-0.75 (-0.89, -0.62)	-0.45 (-0.90, 0.01)	-0.29 (-0.40, -0.18)	-0.70 (-0.92, -0.48)		-0.45 (-0.67, -0.24)				
	4	-0.63 (-0.82, -0.45)	-0.30 (-0.88, 0.27)	-0.20 (-0.33, -0.07)	-0.83 (-1.06, -0.60)		-0.40 (-0.64, -0.16)				

Table S2. 3 continued from above

		Predictors									
Model #	**month**	**step**	**step:chl**	**step:wind**	**turn**	**turn:chl**	**turn:wind**	**df**	**AIC**	**ΔAIC**	**weight**
3	1/overall	0.44 (0.36, 0.52)	-0.03 (-0.06, >0.01)	0.26 (0.17, 0.34)	0.49 (0.33, 0.65)	-0.03 (-0.13, 0.07)	0.38 (0.21, 0.54)	21	19361	2.57	0.12
	2	-0.64 (-0.75, -0.53)		-0.14 (-0.25, -0.03)	-0.45 (-0.67, -0.23)	-0.09 (-0.23, 0.05)	-0.20 (-0.41, 0.02)				
	3	-0.66 (-0.78, -0.55)		-0.30 (-0.41, -0.19)	-0.59 (-0.88, -0.31)	0.49 (-0.44, 1.42)	-0.47 (-0.69, -0.25)				
	4	-0.55 (-0.68, -0.43)		-0.19 (-0.32, -0.06)	-1.09 (-1.42, -0.76)	-1.20 (-2.27, -0.14)	-0.46 (-0.70, -0.21)				
4	1/overall	0.44 (0.35, 0.52)		0.27 (0.18, 0.35)	0.49 (0.33, 0.65)	-0.03 (-0.13, 0.07)	0.38 (0.21, 0.54)	20	19362	3.47	0.07
	2	-0.64 (-0.75, -0.53)		-0.14 (-0.25, -0.03)	-0.45 (-0.67, -0.23)	-0.09 (-0.23, 0.05)	-0.19 (-0.41, 0.02)				
	3	-0.65 (-0.77, -0.54)		-0.31 (-0.42, -0.20)	-0.59 (-0.88, -0.31)	0.49 (-0.44, 1.42)	-0.47 (-0.69, -0.25)				
	4	-0.54 (-0.67, -0.42)		-0.20 (-0.33, -0.07)	-1.09 (-1.42, -0.76)	-1.20 (-2.27, -0.13)	-0.46 (-0.70, -0.21)				
5	1/overall	0.44 (0.36, 0.52)	-0.03 (-0.06, <0.01)	0.26 (0.17, 0.34)	0.50 (0.34, 0.66)	-0.08 (-0.15, -<0.01)	0.36 (0.20, 0.52)	18	19362	3.82	0.06
	2	-0.64 (-0.75, -0.53)		-0.14 (-0.25, -0.03)	-0.47 (-0.69, -0.25)		-0.18 (-0.40, 0.04)				
	3	-0.66 (-0.78, -0.55)		-0.30 (-0.41, -0.19)	-0.70 (-0.92, -0.47)		-0.45 (-0.67, -0.24)				
	4	-0.55 (-0.68, -0.43)		-0.19 (-0.32, -0.07)	-0.83 (-1.06, -0.60)		-0.40 (-0.64, -0.16)				
6	1/overall	0.44 (0.36, 0.53)	-0.06 (-0.12, -0.01)	0.25 (0.16, 0.33)	0.49 (0.22, 0.54)		0.38 (0.33, 0.65)	20	19362	3.93	0.06
	2	-0.65 (-0.76, -0.54)	0.06 (-0.01, 0.13)	-0.12 (-0.23, -0.01)	-0.47 (-0.69, -0.25)		-0.20 (-0.42, 0.02)				
	3	-0.75 (-0.89, -0.62)	-0.45 (-0.90, 0.01)	-0.29 (-0.40, -0.18)	-0.67 (-0.90, -0.45)		-0.48 (-0.70, -0.26)				
	4	-0.63 (-0.82, -0.45)	-0.30 (-0.88, 0.27)	-0.20 (-0.33, -0.07)	-0.80 (-1.03, -0.57)		-0.42 (-0.66, -0.18)				
7	1/overall	0.44 (0.35, 0.52)		0.27 (0.18, 0.35)	0.50 (0.34, 0.66)	-0.08 (-0.15, -0.01)	0.36 (0.20, 0.52)	17	19363	4.78	0.04
	2	-0.64 (-0.75, -0.53)		-0.14 (-0.25, -0.03)	-0.47 (-0.69, -0.25)		-0.18 (-0.39, 0.04)				
	3	-0.65 (-0.77, -0.54)		-0.31 (-0.42, -0.20)	-0.70 (-0.92, -0.48)		-0.45 (-0.67, -0.23)				
	4	-0.54 (-0.67, -0.42)		-0.20 (-0.33, -0.07)	-0.83 (-1.06, -0.60)		-0.40 (-0.64, -0.16)				
8	1/overall	0.44 (0.36, 0.52)	-0.03 (-0.07, <0.01)	0.26 (0.17, 0.34)	0.49 (0.33, 0.65)		0.39 (0.22, 0.55)	17	19364	5.92	0.02
	2	-0.64 (-0.75, -0.53)		-0.13 (-0.25, -0.02)	-0.47 (-0.69, -0.25)		-0.20 (-0.42, 0.02)				
	3	-0.67 (-0.78, -0.55)		-0.30 (-0.41, -0.19)	-0.67 (-0.90, -0.45)		-0.48 (-0.70, -0.26)				
	4	-0.55 (-0.68, -0.43)		-0.19 (-0.32, -0.07)	-0.80 (-1.03, -0.57)		-0.42 (-0.66, -0.18)				

Appendix 3 – Supplementary material for chapter 4

S3. 1 - Determining monthly minimum population size

In order to determine whether sample sizes were sufficient to represent the population-level distribution in each month post-fledging (except October-December as sample sizes were very low; <5 individuals tracked), a resampling procedure was used that iteratively calculated the core use areas for an increasing number of individuals, selected at random, 100 times without replacement. Two non-linear models were fitted to resampled outputs; the two- and three-parameter Michaelis-Menten models within the R package 'drc' (Ritz. & Strebig 2016), as previous studies have indicated that the area occupied reaches an asymptote once a certain number of individuals are included (Soanes et al. 2013; Thaxter et al. 2017). Models were then ranked according to Akaike Information Criterion (AIC) to determine which model fitted the resampled data best (Table S3. 1). As both models performed equally well (were respectively the best fit for two months each), minimum sample sizes were subsequently estimated using both Michaelis-Menten models.

For each month, the core use areas were extrapolated to a 'colony' size of 50 individuals (Table S3. 1 and Fig. S3. 1), as it is rare for more birds to be tracked in a particular breeding stage in any given year. Sufficient individuals were considered to have been tracked at a cut-off of 95% of the core use areas predicted for 50 individuals (Soanes et al. 2013; Thaxter et al. 2017; Clay et al. 2019).

Table S3. 1: Ranking of models used to determine the relationship between sample size and home range area for juvenile grey-headed albatrosses tracked from Bird Island (South Georgia), according to AIC. Best models for each month are in blue. Models compared using AIC are the two- and three- parameter Michaelis-Menten asymptotic exponential models (2MM and 3MM respectively). Minimum predicted sample sizes are shown with 95% confidence intervals in brackets.

			Model selection		Minimum number predicted	
Month	**Sample size**	**Iterations**	**2MM**	**3MM**	**2MM**	**3MM**
May	17	100	**522.6**	523.3	39 (36 - 43)	40 (34 – 45)
June	26	100	**809.4**	810.0	44 (43 – 45)	44 (42 – 45)
July	19	100	583.3	**577.3**	39 (34 – 45)	40 (34 – 47)
August	15	100	437.6	**437.3**	36 (32 – 42)	37 (30 – 46)

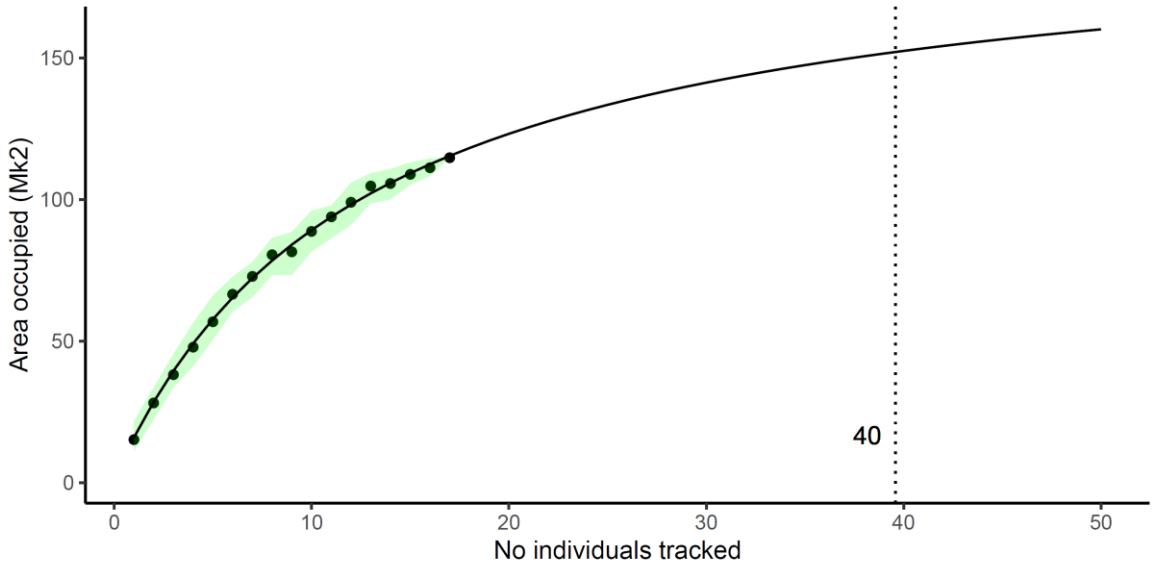

Figure S3. 1: Core area (Mk2 = km^2 x 10^6) as a function of sample size for juvenile grey-headed albatrosses tracked from Bird Island (South Georgia) in May. The fitted asymptotic relationship (three-parameter Michaelis-Menten; black line), median area occupied (black points), and 25% and 75% quantiles (colored, shaded polygon) of 100 resample iterations are shown for the core use area (50%). The predicted minimum sample size is shown by the dashed vertical line.

S3. 2 Fisheries bycatch overlap risk of adult and juvenile GHA

Table S3. 2: The contribution of pelagic longline fleets to the summed overlap score of juvenile grey-headed albatrosses tracked from Bird Island (South Georgia) for May-September and by tuna Regional Fisheries Management Organization (tRFMO; IATTC = Inter-American Tropical Tuna Commission, ICCAT = International Commission for the Conservation of Atlantic Tunas, IOTC = Indian Ocean Tuna Commission and WCPFC = Western and Central Pacific Fisheries Commission). Fleets contributing more than 10% of overlap scores are highlighted in grey. CHN = China, EUESP = Spain, JPN = Japan, KOR = South Korea, MYS = Malaysia, NAM = Namibia, SYC = Seychelles, TWN = Taiwan, VUT = Vanuatu.

tRFMO	Total overlap score (/1000) (Sum May – September)	Fleet contribution (%)									
		CHN	EUESP	JPN	KOR	MYS	NAM	OTHER	SYC	TWN	VUT
All tRFMOS	326.12	0.00	0.02	0.35	0.18	0.00	0.00	0.01	0.03	0.40	-
IATTC	-	-	-	-	-	-	-	-	-	-	-
ICCAT	181.68	-	0.01	0.52	0.29	-	0.01	0.01	-	0.16	-
IOTC	144.44	0.01	0.02	0.13	0.04	0.02	-	0.01	0.07	0.72	-
WCPFC	-	-	-	-	-	-	-	-	-	-	-

Table S3. 3: The contribution of pelagic longline fleets to the summed overlap score of adult grey-headed albatrosses tracked from Bird Island (South Georgia) for May-September and by tuna Regional Fisheries Management Organization (tRFMO; IATTC = Inter-American Tropical Tuna Commission, ICCAT = International Commission for the Conservation of Atlantic Tunas, IOTC = Indian Ocean Tuna Commission and WCPFC = Western and Central Pacific Fisheries Commission). Fleets contributing more than 10% of overlap scores are highlighted in grey. CHN = China, EUESP = Spain, JPN = Japan, KOR = South Korea, MYS = Malaysia, NAM = Namibia, SYC = Seychelles, TWN = Taiwan, VUT = Vanuatu.

tRFMO	Total overlap score (/1000) (Sum May – September)	Fleet contribution (%)									
		CHN	EUESP	JPN	KOR	MYS	NAM	OTHER	SYC	TWN	VUT
All tRFMOS	70.95	0.06	0.01	0.18	0.09	0.02	-	0.11	0.03	0.50	0.02
IATTC	10.04	0.42	0.08	-	-	-	-	0.18	-	0.19	0.13
ICCAT	20.87	-	-	0.36	0.29	-	-	0.12	-	0.23	-
IOTC	39.99	-	-	0.12	-	0.04	-	0.08	0.04	0.71	-
WCPFC	0.053	-	-	-	-	-	-	1.00	-	-	-

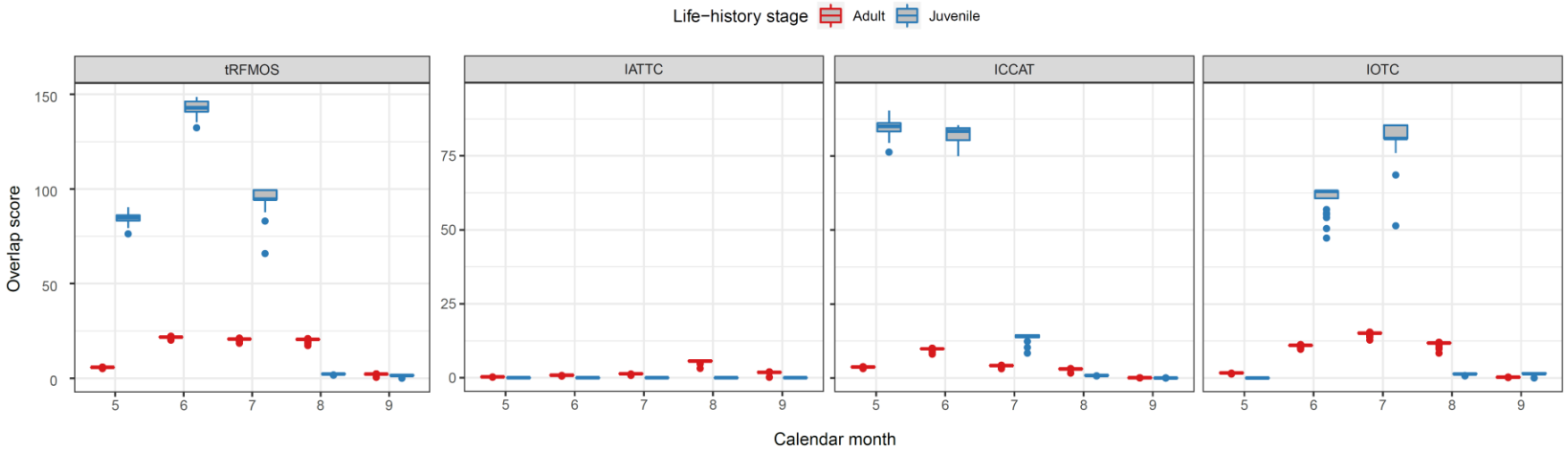

Figure S3. 2: Jackknifed monthly overlap scores (hooks.10^3) of adult and juvenile grey-headed albatrosses tracked from Bird Island, South Georgia, with pelagic longline fishing effort by tuna regional fisheries management organization (tRFMOS; IATTC = Inter-American Tropical Tuna Commission, ICCAT = International Commission for the Conservation of Atlantic Tunas, IOTC = Indian Ocean Tuna Commission).

Appendix 4 – Supplementary material for chapter 5

Table S4. 1: Available sample sizes of processed location and immersion data of black-browed (BBA) and grey-headed (GHA) albatrosses birds of known sex and breeding stage. The sampling interval indicates the setting used for the GPS loggers, or average fix interval for the Platform Terminal Transmitters (PTTs). Trips from birds of known age or of an estimated minimum age greater than the age at which each species shows reproductive senescence (Froy et al. 2017) are in blue font. INC – Incubation, BR – brood-guard

Species	Stage	Season	Device	Sampling interval (minutes)	No. birds	No. trips	Age range	Sex ratio (F:M)	Trips with immersion data	
									High-res	Lower-res
BBA	INC	1997	PTT	224	10 (4)	10 (4)	14 – 24	1 : 3		
		2002	PTT	83	20 (7)	20 (7)	10 – 44	1 : 6		15 (6)
		2015	GPS	30	37 (28)	37 (28)	10 – 36	15 : 13	33 (27)	
	BR	1994	PTT	144	3	4				
		2002	PTT	65	22 (9)	22 (9)	12 – 29	0 : 9		22 (9)
		2005	PTT	116	3	4				
		2008	GPS	5	18 (12)	18 (12)	18 – 29	4 : 8	21 (11)	
		2010	GPS	10	32 (29)	33 (28)	14 – 32	11 : 17	12 (10)	16(16)
		2015	GPS	10	28 (19)	63 (49)	12 – 36	6 : 16	63 (49)	
GHA	INC	1996	PTT	133	3 (1)	3 (1)	38	0 : 1		
		2003	GPS	60	3 (1)	3 (1)	18	1 : 0		
		2003	PTT	57	28 (17)	28 (17)	18 – 45	8 : 9		20 (16)
	BR	1993	PTT	195	1	1				
		1995	PTT	133	6	3				
		2003	PTT	54	28 (7)	17 (12)	10 – 45	2 : 5		27 (11)
		2010	GPS	30	26 (17)	29 (20)	10 – 45	3 : 14	9 (6)	15 (14)
		2012	GPS	10	23 (14)	25 (14)	15 – 30	8 : 6		27 (27)

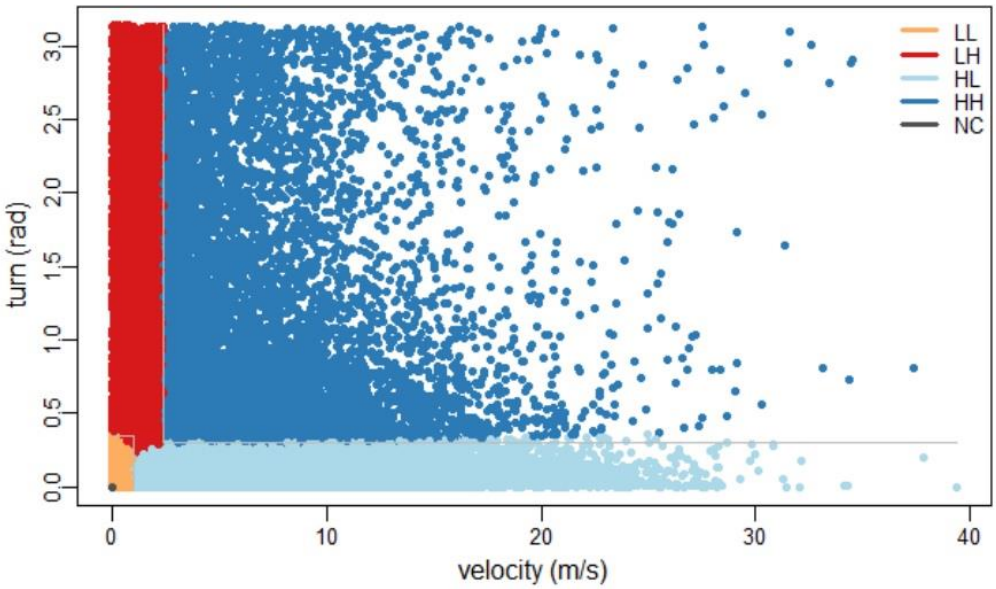

Figure S4. 1: Clustering scatterplot of trip locations according to states identified using EMbC. 'L' and 'H' indicate low and high values of local turning angle and velocity values. Behaviours LH and HH were subsequently merged. NC represents the first point of each trip, which the algorithm did not classify, re-labelled as behaviour HL.

Table S4. 2: Verification of the EMbC population-level analysis using information on the (1) proportion of all trips classified as states 1-3, (2) proportion of total landings occurring in each state, (3) proportion of time spent wet in each state, and (4) mean landing rate (wet events per hour) during each state. This table summarises the characteristics of 74 trips with corresponding immersion data.

States	Behaviour	Prop. trips	Prop. total landings	Mean prop. wet	Mean landing rate
1	Resting	0.17	0.18	0.69	0.27
2	Foraging	0.40	0.50	0.39	0.32
3	Transit	0.43	0.33	0.23	0.20

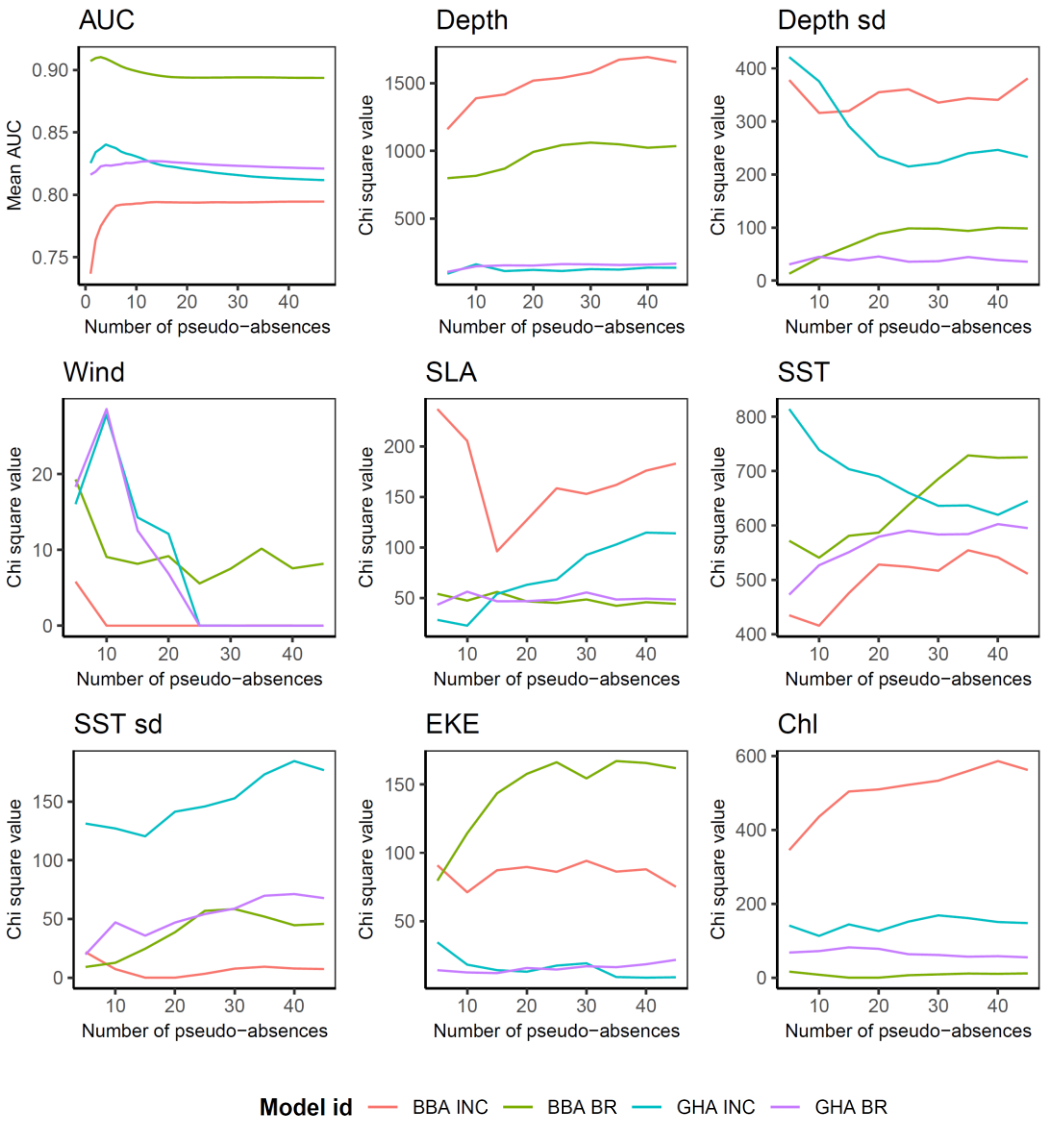

Figure S4. 2: Mean Area Under the Curve (AUC; first plot) and Chi square value (all other plots) of environmental predictor variables for an increasing number of pseudo-absences (between 1 and 47) for the four models predicting the habitat preferences of black-browed (BBA) and grey-headed (GHA) albatrosses in the incubation (INC) and brood-guard (BR) stages. 'Depth' is bathymetry, 'Depth sd' is bathymetric slope, 'Wind' is wind speed, 'SLA' is sea level anomaly, 'SST' is sea surface temperature, 'SST sd' is the standard deviation of SST, 'EKE' is eddy kinetic energy and 'Chl' is chlorophyll concentration.

Table S4. 3: Effect of age, sex, stage, species and year on trip characteristics and activity patterns of black-browed and grey-headed breeding at Bird Island, South Georgia. 'x' indicates terms retained in the most supported models for each response variable (< 2Δ AICc of the top model). AICc= Akaike information criterion model score; ΔAICc = difference in Akaike information criterion score between models; w=Akaike information criterion weights calculated for the set of most supported models.

		Predictor variables																		
Response variable	**n**	Age	Age^2	Sex	Stage	Species	Year	Age: Sex	Age^2: Sex	Age: Stage	Age^2: Stage	Age: Species	Age^2: Species	Sex: Stage	Sex: Species	Stage: Species	**df**	**AICc**	**ΔAICc**	**w**
Trip duration (days)	158	x	x	x	x	x				x	x	x					10	213.5	0.000	0.569
		x	x	x	x	x				x	x						9	214.1	0.553	0.431
Max range from colony (km)	158			x	x	x	x								x		12	338.69	0.000	1.000
Latitude at max range (°)	158	x	x	x	x	x				x	x	x		x		x	12	874.2	0.000	0.448
		x	x	x	x	x				x		x		x		x	11	874.9	0.688	0.317
		x	x	x	x	x				x	x			x		x	11	875.5	1.287	0.235
Landings.hr^{-1} in daylight[a]	66	x		x			x										6	69.76	0.000	0.535
		x					x										5	71.42	1.658	0.233
		x		x				x									5	71.43	1.674	0.232
Landings.hr^{-1} in darkness[a]	64						x										4	116.0	0.000	1.000

Table S4. 3 continued

		Predictor variables																		
Response variable	**n**	Age	Age^2	Sex	Stage	Species	Year	Age: Sex	Age^2: Sex	Age: Stage	Age^2: Stage	Age: Species	Age^2: Species	Sex: Stage	Sex: Species	Stage: Species	**df**	**AICc**	**ΔAICc**	**w**
Wet bout length in daylight (mins)[a]	66	x		x													4	97.77	0.000	1.000
Wet bout length in darkness (mins)[a]	64			x			x										5	144.8	0.000	0.523
							x										4	146.1	1.238	0.282
		x		x	x									x			6	146.8	1.978	0.195
Prop daylight wet (%)	130					x	x										8	199.3	0.000	1.000
Prop darkness wet (%)	128			x	x	x	x										10	314.8	0.000	0.386
					x	x	x										9	315.1	0.325	0.328
						x	x										8	315.4	0.608	0.285

[a] Species was not included in the model for these two metrics as sample size was very small for GHA.

Table S4. 4: Parameter estimates and standard errors (SE) for the best-supported models, predicting the trip characteristics and activity patterns of black-browed and grey-headed albatrosses breeding at Bird Island, South Georgia as presented in Table 5. 2. Parameter estimates and SEs are also shown for the average of the best-supported-models (if >1 best-supported model) as presented in Figures 5. 3-5.

		Estimate ± SE			
Variable	**n**	**Model 1**	**Model 2**	**Model 3**	**Model average**
sqrt (Trip duration)	158				
Intercept		4.760 ± 0.545	4.604 ± 0.540		4.693 ± 0.548
Age		-0.159 ± 0.041	-0.140 ± 0.039		-0.151 ± 0.041
Age^2		0.003 ± 0.001	0.003 ± 0.001		0.003 ± 0.001
Sex (Female)		0.205 ± 0.077	0.207 ± 0.078		0.206 ± 0.077
Species (GHA)		0.701 ± 0.293	0.238 ± 0.080		0.501 ± 0.323
Stage (Brood-guard)		-3.018 ± 0.709	-2.866 ± 0.707		-2.953 ± 0.712
Age : Species (GHA)		-0.019 ± 0.012	-		-0.011 ± 0.013
Age : Stage (Brood-guard)		0.126 ± 0.055	0.115 ± 0.054		0.121 ± 0.055
Age^2: Stage (Brood-guard)		-0.002 ± 0.001	-0.002 ± 0.001		-0.002 ± 0.001
log(Maximum range)	158				
Intercept		6.456 ± 0.339			
Year (2002)		0.361 ± 0.395			
Year (2003)		-0.217 ± 0.429			
Year (2008)		-0.130 ± 0.420			
Year (2010)		0.095 ± 0.395			
Year (2012)		0.328 ± 0.473			
Year (2015)		-0.401 ± 0.360			
Sex (Female)		0.824 ± 0.146			
Species (GHA)		0.879 ± 0.218			
Stage (Brood-guard)		-1.053 ± 0.155			
Sex (Female) : Species (GHA)		-0.838 ± 0.244			
Latitude at maximum range	158				
Intercept		-69.554 ± 4.426	-64.910 ± 3.488	-70.902 ± 4.401	-68.398 ± 4.807

Table S4. 4 continued

Variable	n	Estimate ± SE			
		Model 1	**Model 2**	**Model 3**	**Model average**
Age		1.107 ± 0.328	0.742 ± 0.249	1.281 ± 0.317	1.032 ± 0.368
Age^2		-0.015 ± 0.006	-0.008 ± 0.005	-0.01 ± 0.005	-0.014 ± 0.007
Sex (Female)		7.726 ± 1.041	7.682 ± 1.047	7.716 ± 1.049	7.710 ± 1.045
Species (GHA)		2.128 ± 2.802	2.466 ± 2.813	-2.535 ± 1.231	1.139 ± 3.248
Stage (Brood-guard)		13.978 ± 5.746	5.107 ± 2.332	15.210 ± 5.753	11.453 ± 6.575
Age : Species (GHA)		-0.180 ± 0.097	-0.199 ± 0.097	-	-0.143 ± 0.117
Age : Stage (Brood-guard)		-1.006 ± 0.438	-0.283 ± 0.091	-1.104 ± 0.438	-0.799 ± 0.509
Age^2 : Stage (Brood-guard)		0.014 ± 0.008	-	0.015 ± 0.008	0.010 ± 0.009
Sex (Female) : Stage (Brood-guard)		-5.264 ± 1.296	-5.218 ± 1.304	-5.201 ± 1.306	-5.235 ± 1.301
Species (GHA) : Stage (Brood-guard)		5.452 ± 1.458	5.581 ± 1.465	5.984 ± 1.441	5.618 ± 1.472
log(Landing rate during daylight)	66				
Intercept		1.436 ± 0.229	1.316 ± 0.225	1.219 ± 0.269	1.358 ± 0.254
Age		-0.020 ± 0.008	-0.017 ± 0.008	-0.007 ± 0.010	-0.016 ± 0.010
Year (2010)		-0.161 ± 0.174	-0.173 ± 0.178	-	-0.126 ± 0.168
Year (2015)		0.179 ± 0.130	0.165 ± 0.132	-	0.135 ± 0.136
Sex (Female)		-0.192 ± 0.097	-	0.449 ± 0.398	0.002 ± 0.329
Age : Sex (Female)		-	-	-0.026 ± 0.016	-0.006 ± 0.014
log(Landing rate during darkness)	**64**				
Intercept		0.439 ± 0.173			
Year (2010)		0.676 ± 0.258			
Year (2015)		0.275 ± 0.193			
log(Wet bout duration in daylight)	**66**				
Intercept		0.956 ± 0.257			
Age		0.030 ± 0.010			
Sex		0.269 ± 0.122			
log(Wet bout duration in darkness)	**64**				
Intercept		2.742 ± 0.224	2.864 ± 0.219	0.150 ± 0.463	2.535 ± 0.585
Year (2010)		-0.803 ± 0.320	-0.776 ± 0.326	-	-0.639 ± 0.427
Year (2015)		-0.235 ± 0.240	-0.205 ± 0.244	-	-0.181 ± 0.235

Table S4. 4 continued

Variable	n	Estimate ± SE			
		Model 1	**Model 2**	**Model 3**	**Model average**
Sex (Female)		0.334 ± 0.180	-	0.912 ± 0.300	0.353 ± 0.361
Age		-	-	0.027 ± 0.015	0.005 ± 0.013
Stage (Brood-guard)		-	-	0.428 ± 0.262	0.083 ± 0.205
Sex (Female) : Stage (Brood-guard)		-	-	-0.927 ± 0.388	-0.180 ± 0.405
logit(Prop daylight wet)	**130**				
Intercept		-1.624 ± 0.139			
Year (2003)		1.197 ± 0.245			
Year (2008)		1.041 ± 0.205			
Year (2010)		0.927 ± 0.174			
Year (2012)		1.482 ± 0.258			
Year (2015)		1.060 ± 0.162			
Species (GHA)		-0.419 ± 0.166			
logit(Prop darkness wet)	**128**				
Intercept		-2.192 ± 0.269	-2.142 ± 0.269	-1.899 ± 0.221	-2.092 ± 0.285
Year (2003)		1.824 ± 0.406	1.933 ± 0.403	1.764 ± 0.391	1.843 ± 0.406
Year (2008)		0.842 ± 0.334	0.925 ± 0.332	1.033 ± 0.327	0.924 ± 0.340
Year (2010)		0.946 ± 0.286	1.025 ± 0.284	1.133 ± 0.277	1.025 ± 0.293
Year (2012)		0.489 ± 0.423	0.649 ± 0.413	0.757 ± 0.410	0.618 ± 0.431
Year (2015)		1.602 ± 0.280	1.691 ± 0.276	1.541 ± 0.260	1.614 ± 0.279
Sex (Female)		0.240 ± 0.151	-	-	0.093 ± 0.150
Species (GHA)		0.646 ± 0.263	0.610 ± 0.263	0.610 ± 0.265	0.624 ± 0.264
Stage (Brood-guard)		0.396 ± 0.224	0.351 ± 0.224	-	0.268 ± 0.255

Table S4. 5: Effect of age, sex, stage, species and year on trip characteristics and activity patterns of black-browed and grey-headed breeding at Bird Island, South Georgia. 'x' indicates terms retained in the most supported models (top 5 are shown here) ranked according to Leave One Out Cross Validation (Loocv). AICc values are shown for comparison, and the most supported models chosen according to AICc are highlighted in blue for each response variable.

		Predictor variables																	
Response variable	**n**	Age	Age^2	Sex	Stage	Species	Year	Age: Sex	Age^2: Sex	Age: Stage	Age^2: Stage	Age: Species	Age^2: Species	Sex: Stage	Sex: Species	Stage: Species	**df**	**Loocv**	**AICc**
Trip duration (days)	158	x	x	x	x	x				x	x	x					10	0.473	213.5
		x	x	x	x	x				x	x						9	0.476	214.1
		x	x	x	x	x											7	0.477	215.1
		x	x		x	x				x	x	x					9	0.483	218.5
		x	x	x	x					x	x						8	0.484	221.0
Max range from colony (km)	158			x	x	x	x								x	x	13	0.697	339.0
				x	x	x	x								x		12	0.698	338.7
				x	x	x									x	x	7	0.708	344.1
				x	x	x									x		6	0.712	344.7
				x	x	x	x									x	12	0.716	346.8
Latitude at max range (°)	158	x	x	x	x	x				x	x	x		x		x	12	3.888	874.2
		x	x	x	x	x				x	x			x		x	11	3.890	875.5
		x	x	x	x	x				x		x		x		x	11	3.911	874.9

Table S4. 5 continued

		Predictor variables																	
Response variable	**n**	Age	Age^2	Sex	Stage	Species	Year	Age: Sex	Age^2: Sex	Age: Stage	Age^2: Stage	Age: Species	Age^2: Species	Sex: Stage	Sex: Species	Stage: Species	**df**	**Loocv**	**AICc**
Latitude at max range (°) - Continued	158	x		x	x	x						x		x		x	10	3.913	876.2
		x	x	x	x	x				x				x		x	10	3.927	877.0
Landings.hr^{-1} in daylight*	66	x		x			x										6	0.404	69.76
		x		x				x									5	0.407	71.43
		x		x													4	0.410	71.92
		x					x										5	0.411	71.42
		x															3	0.413	73.11
Landings.hr^{-1} in darkness*	64						x										4	0.589	116.0
																	2	0.600	118.4
Wet bout duration in daylight (mins)*	66	x		x													4	0.499	97.77
		x															3	0.509	100.3
				x													3	0.526	105.0
																	2	0.530	105.6
Wet bout duration in darkness (mins)*	64	x		x	x		x							x			8	0.729	145.6
				x			x										5	0.732	144.8
							x										4	0.740	146.1
		x		x	x				x					x			7	0.744	147.2

Table S4. 5 continued

Response variable	n	Predictor variables															df	Loocv	AICc
		Age	Age^2	Sex	Stage	Species	Year	Age: Sex	Age^2: Sex	Age: Stage	Age^2: Stage	Age: Species	Age^2: Species	Sex: Stage	Sex: Species	Stage: Species			
		x		x	x									x			6	0.774	146.8
Prop daylight wet (%)	130	x	x	x		x	x	x	x								13	0.514	199.5
						x	x										8	0.518	199.3
		x	x	x			x	x									12	0.519	203.5
							x										7	0.524	203.6
		x	x	x				x	x								7	0.553	219.9
Prop darkness wet (%)	128			x	x	x	x									x	11	0.815	315.4
						x	x										8	0.815	315.4
							x										7	0.827	318.6
				x	x	x									x	x	7	0.907	341.4
				x	x	x										x	6	0.909	341.7

Appendix 5 – Supplementary material for chapter 6

Table S5. 1: ProbGLS algorithm parameters used to compute white-chinned petrel (*Procellaria aequinoctialis*) foraging trip locations from twilight events. Fifteen incubating adults were tracked from Bird Island, South Georgia, during the 2009/2010 breeding season.

Model parameter	Description	Value used
particle.number	Number of particles computed for each point cloud	10 000[a]
Iteration.number	Number of track iterations	200[a]
sunrise.sd & sunset.sd	Shape, scale and delay values describing the assumed	2.49/0.94/0[a]
range.solar	Range of solar angles used	-7° to -1°[a]
boundary.box	The range of longitudes and latitudes likely to be used by tracked individuals	Lon (-100°, 10°) & Lat (-80°, 0°)[b]
days.around.spring.equinox & days.around.fall.equinox	Number of days before and after an equinox event in which a random latitude will be assigned	14/21 (spring) & 21/14 (fall)[c]
speed.dry	Fastest most likely speed, speed standard deviation and maximum speed allowed when the logger is not submerged in sea water	10.23/3.72/17.94 $m.s^{-1}$ [d]
speed.wet	Fastest most likely speed, speed standard deviation and maximum speed allowed when the logger is submerged in sea water	0.78/1.09/3.56 $m.s^{-1}$ [d]
sst.sd	NULL	0.5°C[e]
max.sst.diff	NULL	3°C[a]
east.west.comp	Compute longitudinal movement compensation for each set of twilight events	Used[a]

[a] Same values as in Merkel et al. (2016), which involved the same geolocator model and similar foraging areas as in this study (South Georgia and Patagonian Shelf)

[b] Encompasses southwest Atlantic, Patagonian Shelf and west coast of South America (Phillips et al. 2006)

[c] Number of days chosen following manufacturer's instructions

[d] Calculated from white-chinned petrel GPS tracks and associated immersion data from in the 2014/2015 breeding season

[e] Logger-temperature accuracy

Table S5. 2: Time Depth-Recorder (TDR) sampling regime for 14 incubating white-chinned petrel adults tracked from Bird Island (South Georgia) during the 2009/2010 breeding season. TDRs were set to continuously record depth at coarser temporal scales (1 or 5s time intervals, indicated below for each ring-date combination in the 'I' column) every day (rings 702-705) or every third day (rings 341-702). TDRs were also set to record high-resolution depth data (0.5 s) using the fast-logging mode, which is activated when an animal enters water. Dates for which there is fast-logging data are indicated by an 'x' in the 'FL' column for each ring-date combination.

	White-chinned petrel ring IDs (abbreviated)																									
Date	**341**		**342**		**343**		**344**		**345**		**346**		**347**		**348**		**350**		**701**		**702**		**703**		**704**		**705**	
	I	**FL**	**I**	**FL**	**I**	**FL**	**I**	**FL**	**I**	**FL**	**I**	**FL**	**I**	**FL**	**I**	**FL**	**I**	**FL**	**I**	**FL**	**I**	**FL**	**I**	**FL**	**I**	**FL**
06 – Dec – 2009	1	x	1		1		1		1		1	x	1		1	x	1	x	1								
07 - Dec – 2009																										
08 – Dec – 2009																										
09 – Dec – 2009	1	x	1		1	x	1	x	1	x	1	x	1		1	x	1	x	1								
10 – Dec – 2009																										
11 – Dec – 2009																										
12 – Dec – 2009	1	x	1	x	1	x	1		1	x	1	x	1		1	x	1	x	1								
13 – Dec – 2009																										
14 – Dec – 2009																										
15 – Dec – 2009	1	x	1	x	1	x	1	x	1	x	1	x	1		1	x	1	x	1								
16 – Dec – 2009																										
17 – Dec – 2009																										

Table S5. 2 continued

Date	White-chinned petrel ring IDs (abbreviated)																									
	341		342		343		344		345		346		347		348		350		701		702		703		704		705	
	I	FL	I	FL	I	FL	I	FL	I	FL	I	FL	I	FL	I	FL	I	FL	I	FL	I	FL	I	FL	I	FL	I	FL
18 – Dec – 2009	1	x	1	x	1	x	1	x	1	x	1		1	x	1	x	1	x	1	x										
19 – Dec - 2009																												
20 – Dec – 2009																												
21 – Dec- 2009	1	x	1	x	1	x	1	x	1		1	x	1	x	1	x	1		1	x										
22 – Dec – 2009																												
23 – Dec - 2009																					1		1		1		1	
24 – Dec – 2009			1	x			1				1	x	1	x					1	x	5		5		5	x	5	
25 – Dec – 2009																					5		5		5	x	5	
26 – Dec – 2009																					1		1	x	1	x	1	
27 - Dec – 2009			1				1	x			1	x	1	x					1	x	5		5	x	5	x	5	
28 – Dec – 2009																					5		5	x	5	x	5	x
29 – Dec – 2009																					1		1	x	1	x	1	x
30 – Dec – 2009																					5		5	x	5	x	5	x
31 – Dec – 2009																					5		5	x	5	x	5	x
01 – Jan – 2010																					1	x	1	x	1		1	x

Table S5. 2 continued

Date	White-chinned petrel ring IDs (abbreviated)																							
	341		342		343		344		345		346		347		348		350		701		702		703		704		705	
	I	FL	I	FL	I	FL	I	FL	I	FL	I	FL	I	FL	I	FL	I	FL	I	FL	I	FL	I	FL	I	FL	I	FL
02 – Jan – 2010																					5	x	5	x	5	x	5	x
03 – Jan – 2010																					5	x	5	x	5	x	5	x
04 – Jan – 2010																					1	x	1	x	1	x	1	x
05 – Jan -2010																					5	x	5	x	5	x	5	x
06 – Jan – 2010																					5	x	5	x	5	x	5	x
07 – Jan – 2010																					1	x	1	x	1	x	1	x
08 – Jan – 2010																					5	x	5	x	5	x	5	x
09 – Jan – 2010																					5	x	5	x	5	x	5	x
10 – Jan – 2010																					1	x	1	x	1	x	1	
11 – Jan – 2010																					5	x	5		5	x	5	
12 – Jan – 2010																					5	x	5		5	x	5	
13 – Jan – 2010																					1	x						
14 – Jan – 2010																					5	x						
15 – Jan – 2010																					5							
16 – Jan – 2010																					1							

Table S5. 3: Comparison of dives recorded using the continuous pressure and fast-logging recording modes of Time-Depth Recorders (TDRs) deployed on 14 incubating white-chinned petrels tracked from Bird Island (South Georgia) during the 2009/10 breeding season.

Data recording mode	Total number of dives recorded	Number of dives post-filtering[a]	Matching dives[b]	Number of non-matching dives with 1 data point	Number of non-matching dives <2m, <3m and <4m depth	Short dives missed by continuous pressure mode
Continuous pressure mode	1804	1656	838	536	772, 812, 816	
Fast-logging mode	1079	895	845			29

[a] Dives recorded using both modes were filtered to reduce further noise by removing (1) very short dives (<1s), (2) very long dives (this occurred in the continuous pressure recording mode when dives were incorrectly offset), and (3) very deep dives with a small number of data points (<4).

[b] Matching dives refers to dives in the continuous pressure mode which match in terms of timings with dives in the fast-logging mode in row 1, and vice versa in row 2.

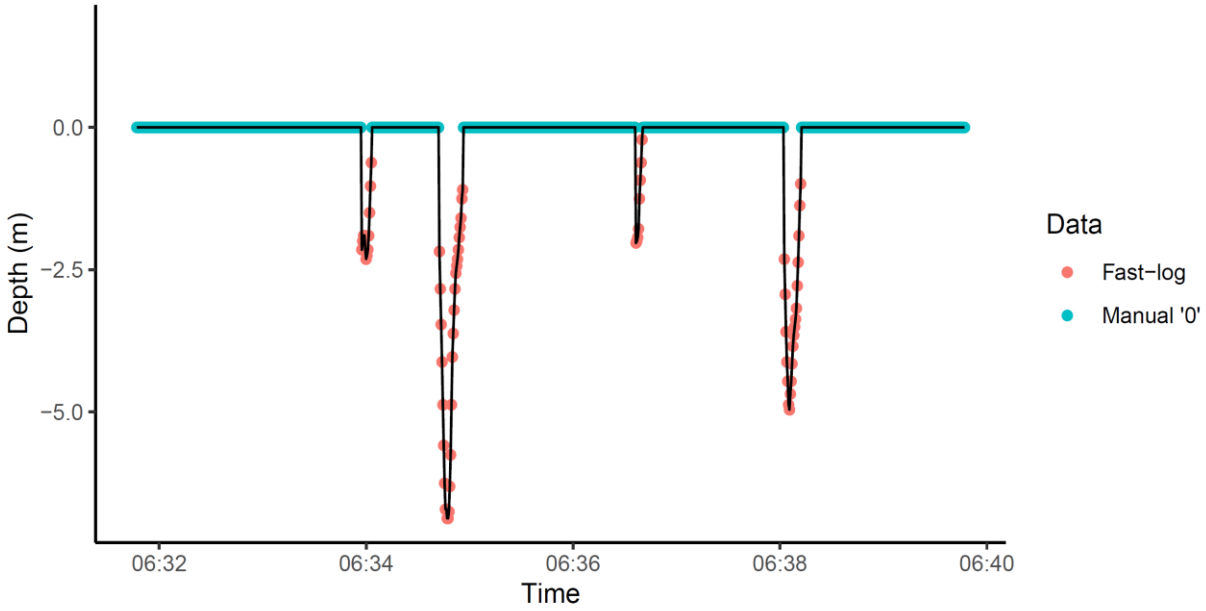

Figure 5. S1: Example of manual interpolation of fast-log data recorded using Time-Depth Recorders deployed on 14 incubating white-chinned petrels from Bird Island (South Georgia) during the 2009/10 breeding season. Fast-log depth recordings were interpolated with manual '0's for further processing within the 'diveMove' package.

Table S5. 4: Published and advised (highlighted in blue) at-sea line sink rates in pelagic and demersal longline fishing vessels operating within the Southern Ocean. Fastest recorded sink rates are shown per publication and were converted to $m.s^{-1}$ if necessary. Sink rates are ordered from fastest to lowest per 'longline type' (demersal vs. pelagic longline fishing).

Longline type	Recorded sink rate ($m.s^{-1}$)	Specific gear configuration	Factors affecting sink rate	Setting speed (knots)	Fleet & target species	Reference
Demersal						
Chilean	1.47 (2-5m depth)	6kg steel weights at 40m intervals + removal of hook line present in Spanish system to avoid depredation	Steel weights sank faster than rocks.	6	Chilean (Patagonian toothfish)	Robertson et al. 2008b
Traditional bottom longline	0.22-0.69 (15m depth)	200-600g weights on secondary lines and 25-30kg anchor	Sink rates faster close to first anchor, and slower on last section of mother line.	4-6.5	Artisanal Chilean (Patagonian toothfish)	Moreno et al. 2006
Autoline/single-line	0.16-0.50 (0-5m depth) 0.15-0.70 (5-10m depth)	5kg per 400m	Sink rates varied across the line, and were fastest in the middle.	6-6.5	New Zealand (ling)	Smith 2001
Autoline/single-line	0.44 (0-4m depth) 0.37 (4-8m depth) 0.37 (8-12m depth)	6.5kg weights 35m intervals	Sink rate decreased with increasing weight spacing.	5.5-6.5	British (Patagonian toothfish)	Robertson, 2000
Spanish/double-line	0.33 (0-2m depth) 0.80 (2-5m depth)	8kg steel weights at 40m intervals	Steel weights sank faster than rocks.	6	Spanish (Patagonian toothfish)	Robertson et al. 2008b
Vertical longline (anchored & free-floating lines)	0.33 (15m depth)	0.3-1.0kg weight on mother line		Stationary	Artisanal Chilean (hake)	Moreno et al., 2006
Spanish/double-line	0.28 (0-4m depth) 0.33 (4-8m depth) 0.32 (8-12m depth)	3.6kg weights at 38m intervals		10-10.5	Korean (Patagonian toothfish)	Robertson, 2000
Spanish/double-line	0.26 (2m depth) 0.61 (15m depth)	8k weights at 30m intervals	Most powerful effect on sink rate was line weighting, which affected sink rate independent of setting speed.	6	Spanish (Patagonian toothsfish)	Robertson et al. 2008a

Table S5. 4 continued

Longline type	Recorded sink rate ($m.s^{-1}$)	Specific gear configuration	Factors affecting sink rate	Setting speed (knots)	Fleet & target species	Reference
Autoline/single-line, Spanish/double-line and Chilean	0.3 (10m depth) >=0.24 (10m depth) 0.3 (10m depth)	Autoline, Spanish and Chilean: 5kg steel weights at 40m intervals Autoline-only: $50g.m^{-1}$ integrated weights Autoline: 5kg steel weights at 50-60m intervals or $50g.m^{-1}$ integrated weights Spanish: 8.5kg at 40m intervals/ 6kg at 20m intervals (rock or concrete weights), or 5kg at 40m intervals (steel weights) Chilean: 6kg (rock or concrete) or 5k (steel) weights at distal end of line Mix of Spanish and Chilean: Spanish weighting as above and 8.5kg (rock or concrete)/5kg (steel) weights at 80m intervals				ACAP 2017 CCAMLR 2018, 2019
Autoline/single-line	0.25 (0-20m depth)	$50g.m^{-1}$ integrated weights (beaded lead core)	Lines with integrated weights sank faster than unweighted lines.	6-6.5	New Zealand (ling & Patagonian toothfish)	Robertson et al., 2006
Autoline/single-line	0.25 (2m depth)	$50g.m^{-1}$ integrated weights (lead core)	Line setter did not significantly change sink rate.	6-6.5	Commercial auto-liner	Robertson et al. 2008c
Autoline/single-line	0.24 (15m depth)	$50g.m^{-1}$ integrated weights			New Zealand	Wienecke & Robertson, 2004
Pelagic						
	1.13 (2 seconds) 0.09 (3-30 seconds) 0.22 (30-55 seconds)	No swivel, baited branchlines hand-thrown.	Hand-thrown baited branchlines initially sank fast, but slowed down quite quickly.	8-10	New Zealand (tuna sp.)	O'Toole & Molloy 2000
	0.51 (0-2m depth) 0.61 (2-5m depth) 0.61 (5-8m depth)	60g safe-lead swivels at the hook Monofilament mainline set through a line shooter in the surface set tight configuration		8	Australian (tuna and swordfish sp.)	Robertson, Candy & Hall, 2013

Table S5. 4 continued

Longline type	Recorded sink rate ($m.s^{-1}$)	Specific gear configuration	Factors affecting sink rate	Setting speed (knots)	Fleet & target species	Reference
	0.47 (0-2m depth) 0.47 (2-5m depth) 0.52 (5-10m depth)	60g safe-lead swivel at 70cm from hook	Weighted branchlines sank faster than unweighted branchlines.	9.5	Japanese (tuna and swordfish sp.)	Melvin et al. 2013
	0.45 (20m depth)	60g lead swivel at 5m from hook	Sink rate increased with addition of a lead swivel within 5m of the hook, with increasing wind speed, and use of partially thawed baits.	7	New Zealand (tuna sp.)	Anderson & Mcardle 2002
	Achieve >=0.4 (0-2m depth)	60g at <=1m from hook 40g at <=0.5m from hook 80g at <=2m from hook				ACAP 2019
	0.32 (0-1m depth) 0.38 (1-2m depth) 0.43 (2-3m depth) 0.42 (3-4m depth) 0.38 (4-5m depth)	60g weighted lead swivels	Tight mainline initially sank faster than other set-ups but all types reached same sink rate by 5m depth.	7-7.3	Australian (tuna and swordfish sp.)	Robertson, Candy & Wienecke, 2010a
	0.31 (0-2m depth) 0.35 (2-4m depth) 0.35 (4-6m depth) 0.28 (6-10m depth)	65 weighted lead swivel at 1m from hook		7.5	Uruguayan (tuna, swordfish and shark sp.)	Jiménez et al. 2019
	0.29 (0-3m depth) 0.37 (3-6m depth)	75g leaded swivel at 3m from hook Mainline set in surface set tight configuration	No strong effects of bait landing position on sink rates. Main differences in sink rates are due to vessel differences in branch line design, bait size and propeller diameters.	8.5	Stern-set tuna and swordfish sp. longliners with square chinned transoms	Robertson & Candy 2014
	0.28 (0-2m) 0.49 (2-4m) 0.52 (4-6m) 0.48 (6-10m)	Electric fishing light (160g) + 60-75 g leaded swivels at 3.5-5.5m from hooks	Fastest sink rates achieved with 3.5m leader length. Addition of Electric Fishing Light (EFL) did not increase sink rate.	6	Brazilian (tuna, swordfish and shark sp.)	Gianuca, Sant'Ana & Neves, 2016
	0.27 (0-2m depth) 0.74 (4-6m depth)	160g weighted lead swivel at 2m from hook Mainline set in a 'surface set tight' configuration	Fastest initial and final sink rates achieved with heavy swivels placed closed to hooks.	8	Australian (tuna and swordfish sp.)	Robertson et al. 2010b

Table S5. 4 continued

Longline type	Recorded sink rate ($m.s^{-1}$)	Specific gear configuration	Factors affecting sink rate	Setting speed (knots)	Fleet & target species	Reference
	0.26 (10m depth)	Double weighted-branchline (65-70g total weight) at 2m from the hook		9.8	Japanese (tuna and swordfish sp.)	Melvin et al. 2014
	0.19 (0-2m depth) 0.40 (2-4m depth) 0.42 (4-10m depth)	60g lumo lead at 1m from hook	Fastest sinks rates achieved by placing lead closer to the hook.	6	Brazilian (tuna and swordfish sp.)	Santos et al. 2019